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Cover design: The four subjects symbolize the diversity of sciences embraced by the Royal Society of Western Australia. Mangles' kangaroo paw (*Anigozanthos manglesii*) and the numbat (*Myrmecobius fasciatus*) are the floral and faunal emblems of Western Australia, and stromatolites are of particular significance in Western Australian geology (artwork: Dr Jan Taylor). The Gogo Fish (*Mcnamaraspis kaprios*) is the fossil emblem of Western Australia (artwork: Danielle West after an original by John Long).

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Population demography and seed bank dynamics of the threatened obligate seeding shrub *Grevillea maxwellii* McGill (Proteaceae)

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Abstract

Grevillea maxwellii McGill (Proteaceae) is a threatened endemic perennial shrub restricted to the Pallinup River corridor in southern Western Australia. This obligate seeding species was demonstrated to have a low fruit to flower ratio (0.0123) and a small soil-stored seed reserve of 24.4 m^{-2} that remains highly viable (greater than 90 %) for at least 12 months. After disturbance the seedling to parent ratio was 9:1, and the juvenile period for this species was at least four years. Fire and episodic autumn rainfall events appeared to provide the most effective stimuli for recruitment however seedling survival was adversely affected by grazing and drought. Over the study period survival of the largest cohorts of seedlings ranged from 5.3% (after fire treatment) to 8.7% (no disturbance). Percentage mortality of adult plants ranged from 30% to 37% pre-study to 9% to 12% during the study. Inter-fire recruitment was effective in maintaining population stability over the four-year study period however small population size renders this threatened species vulnerable to stochastic environmental events. Too frequent disturbance in combination with low seed production, juvenile period, drought and grazing have the potential to drive this species to extinction.

Keywords: *Grevillea*, fire, germination, conservation, seed production, recruitment, survival, threatened species.

Introduction

Episodic and event dependant recruitment (fire, rainfall, mechanical disturbance) is common in fire-prone ecosystems and has been shown in a range of *Grevillea* species from Australia (*e.g.,* Auld 1995, Auld & Tozer 1995, Auld & Scott 1996, Vaughton 1998, Kenny 2000, Morris 2000, Pickup *et al.* 2003). Germination can be triggered by disturbance that alters the environment around the seed making it favourable for seedling establishment and/or altering the dormancy state of the soil-stored seed reserve (Fenner & Thompson 2005). A species' response to disturbance is determined by life-history attributes such as seed characteristics, seed storage and dispersal, seed availability, and the ability for seedling recruitment and persistence (Noble & Slatyer 1980). For successful regeneration after disturbance, the interval between disturbances must be long enough to allow seedlings to mature and replenish the seed bank, but not so long that seed or adult longevity is exceeded. This juvenile period is a critical stage in the life cycle of the plant. For long-lived woody perennials too frequent disturbance events may increase the risk of local population extinction, particularly if the disturbance occurs during the juvenile period, if annual seed production is low and predation rates are high, or if disturbance events stimulate germination and exhaust the soil-stored seed reserve (Auld 1995; Keith 1996; Regan *et al.* 2003; Auld & Scott 2004). The risk of extinction increases if subsequent seedling survival is low due to drought and grazing.

For obligate seeding species the seed bank strongly influences population dynamics and persistence after disturbance events. Low seed bank size may be due to low fecundity, pre-and post-dispersal seed losses, low seed viability and low seed longevity in the soil. For species with restricted distributions the seed bank size may contribute to rarity. Members of the Proteaceae often have extremely low fruit to flower ratios (0.001–0.163) (Collins & Rebelo 1987), a phenomenon particularly apparent in the genus *Grevillea* (Table 1). Naturally low fruit to flower ratios are a result of interacting factors including pollen and resource limitation, and fruit predation (Stephenson 1981). In many cases, plants adopt a bet hedging strategy where excess flowers help match seed production to resource availability in low resource habitats. This attracts pollinators and ensures fruit set with high pre-dispersal predation (Ehrlen 1993).

Two hundred and twenty-five of the 357 Australian *Grevillea* species (Makinson 2000) occur in Western Australia. The genus is the third largest in the State after *Acacia* (587) and *Eucalyptus* (391) (http://florabase.calm.wa.gov.au/statistics). *Grevillea* species are found throughout all habitats and ecosystems, displaying a variety of forms and life history attributes. Western Australia has 112 listed threatened species and subspecies in this genus (Atkins 2006). The endemic

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Table 1

Habitat, reproductive mode and fruit to flower ratio (FR: FL) in *Grevillea* species.

Species	Habitat	Seeder (S) Resprouter (R)	FR: FL ratio	Citation
G. althoferorum	SW WA sandplain	R	0.0015	Burne *et al.* 2003
G. barklyana	VIC riverine	S	0.019, 0.001–0.053	Vaughton 1995, 1998
G. beadleana	NE NSW riverine	S	0.007 – 0.100	Smith and Gross 2002
G. caleyi	NSW woodland/heath	S	0.0300	(cited in Vaughton 1998)
G. humifusa	SW WA woodland/heath	S/R	0.0900	Harris & Yates 2003
G. leucopteris	SW WA open heath/tall shrubland	S	0.0530	Lamont 1982
G. linearifolia	E NSW woodland	S	0.0150	Hermanutz *et al.* 1998
G. longifolia	NSW sclerophyll forest	S	0.0380	Hermanutz *et al.* 1998
G. maxwellii	SW WA low heath	S	0.0123	Present study
G. mucronulata	E NSW sclerophyll forest	S	0.0320	Hermanutz *et al.* 1998
G. oleoides	S NSW open heath/woodland	S/R	0.0960	Hermanutz *et al.* 1998
G. rudis	SW WA shrubland	S	0.0027	Burne *et al.* 2003
G. sphacelata	Coastal NSW heath /dry sclerophyll woodland	R	0.0260	Hermanutz *et al.* 1998
G. synapheae	SW WA heath/woodland/shrubland	S	0.0037	Burne *et al.* 2003
G. wilsonii	SW WA forest/woodland	S/R	0.0640	(cited in Vaughton 1998)

Western Australian *Grevillea maxwellii* (McGill) is ranked as endangered under the Australian Commonwealth Environment Protection and Biodiversity Conservation Act 1999 (http://www.deh.gov.au/cgi-bin/sprat/public/publicthreatenedlist.pl?wanted=flora) and meets the World Conservation Union (IUCN 2001) Red List Category 'CR' under criteria B1+2ce. Although *G. maxwellii* is endangered and has an Interim Recovery Plan (Phillimore *et al.* 2001), there is no published information on the ecology or biology of the species. Basic census data on abundance is gathered on a regular basis and seedlings have been observed at one population, but their contribution to population stability and persistence is unknown (S. Barrett, unpublished data).

This study investigates some key life history attributes that affect the population dynamics of *Grevillea maxwellii.* We examined population structure, quantified fruit to flower ratio, assessed the magnitude, viability and disturbance response of the soil-stored seed reserve, and determined the factors that affect seedling survival in order to contribute to the management and long-term conservation of the species.

Materials and methods

Study species

Grevillea maxwellii is a small, spreading spring-flowering shrub with lobed leaves and large red inflorescences which shelter beneath the foliage (Olde & Marriott 1995). The species is related to *G. asparagoides, G. batrachioides* and *G. secunda. G. maxwellii* grows in low open heath in shallow brown loamy soil over granite on rocky hilltops and slopes to the Pallinup River east of the Stirling Range in the South West of Western Australia. Plants become rarer as the soil depth increases (Robinson & Coates 1995). The species may be pollinated by nectarivorous birds (Olde & Marriott 1995), although mammal pollination has also been suggested (Obbens 1997). The glandular brown fruits mature over two to three months and contain one ellipsoidal seed c. 9.35 x 3.95 mm in size, with a mean weight of 0.04 g (n = 20). Seeds of *G. maxwellii,* like that of other *Grevillea* species, are released annually. They have no clear dispersal mechanisms, although a narrow waxy wing around the edge of the seed may be attractive to ants. Under controlled conditions dormancy of fresh seeds is broken when the seed coat is damaged by scarification. Smoke application has been found to be beneficial in stimulating germination (A. Cochrane unpublished data). The response of the species to fire has not been studied previously but like many other *Grevillea* species, *G. maxwellii* is considered to be an obligate re-seeder killed by fire with a soil-stored seed bank (Olde & Marriott 1995).

G. maxwellii was originally collected by the explorer and botanist James Drummond in 1840. Another collection was made in 1966 and again in 1986 when the species was known from one population of over 40 plants. With extensive survey in recent years, the species is now known from nine fragmented populations containing less than 1000 plants (pers. comm. S. Barrett). The main threats to the survival of the species are drought and inappropriate fire regimes. At the commencement of the present study all of the nine known populations were long unburnt and considered to be senescing and facing gradual and ongoing decline.

Study sites

Two study sites were chosen east of the Stirling Range National Park and southwest of the Pallinup River. The climate of the area is dry Mediterranean with cool wet winters; hot, dry summers and a mean annual rainfall of 420.5 mm per annum (1968–2006). Mean monthly maximum rainfall of 48.4 mm occurs in July and the mean monthly minimum of 19.1 mm occurs in February. Both sites were determined to be long unburnt (more than 25 years since last fire) based on local knowledge. The response of *G. maxwellii* to disturbance was studied at Site 1 (Unallocated Crown Land (UCL), 34° 16′ S 118° 26′ E) where the longevity of the soil seed bank and fruit to flower ratio were also examined. Just over 100 mature plants occur at this site. The vegetation is low heath on shallow sandy loam over granite. Associated species include *Allocasuarina campestris, Calothamnus quadrifidus, Hakea marginata, Gastrolobium spinosum, Melaleuca hamata, Calytrix tetragona* and *Borya sphaerocephala*. The second site, where seedling survival in the absence of disturbance was studied, was on private property (34° 18' S 118° 30' E) where approximately 50 mature plants were located in open *Allocasuarina huegeliana* woodland over low open heath with *Hypocalymma angustifolium, Calothamnus quadrifidus, Hakea lissocarpha, Stypandra glauca* and *Borya sphaerocephala*. Soils here are generally shallower than those of Site 1 with a greater percentage cover of bare rock. Monthly rainfall data was obtained from adjacent property owners for the duration of the study period.

Life history and population structure

At the commencement of the study in 2001/2002 and again in 2006, the size and structure of each population was determined by walking transects through the population. Plants were allocated to one of four age classes: living large mature (canopy area > 0.5 x 0.5 m), young mature (canopy area < 0.5 x 0.5 m, > 0.2 x 0.2 m), and juvenile plants (< 0.2 x 0.2 m) and dead plants. As growth of mature plants was primarily horizontal with little vertical growth, plant height was not considered to be a useful indicator of age. Young seedlings at the cotyledon stage were not recorded in these transects.

Seed production

Seed production was examined at Site 1 over one flowering season in 2004. Three stem sections were sampled on each of 10 randomly selected mature plants in 2 m x 2 m quadrats established to monitor the effect of disturbance. Stem sections were approximately 10 cm in length. At the commencement of the reproductive phase the total number of inflorescence buds in each section was counted. In November 2004, the total number of mature fruit was then recorded. Fruit set for *G. maxwellii* was compared with that of other *Grevillea* species documented in the literature (Table 1).

Soil Seed Bank

To investigate the distribution and magnitude of the soil seed bank a total of 40 soil samples (15 cm x 15 cm x 20 mm) were collected from beneath the canopy of 20 randomly selected plants (10 live and 10 dead) at each site. Samples were air dried and passed through a series of different sized sieves. Gravel and larger rocks and litter were fractioned off, removed and soil aggregations broken up until two fractions remained above and below the normal size range of *G. maxwellii* seeds. The fraction below the size range was discarded; the remaining fraction was examined for *G. maxwellii* seeds. The viability of seeds retrieved from the soil-stored seed bank was assessed under conditions that have been implicated in the stimulation of germination of other *Grevillea* species (e.g., Dixon *et al.* 1995; Kenny 2000, Morris 2000; Morris *et al.* 2000; Pickup *et al.* 2003). Seeds were pre-treated with smoked water for 2 hours, rinsed, then manually scarified along the longitudinal axis with a sharp scalpel knife and placed on a 1% w/v agar solution in 9 mm glass petrie dishes. Seeds were incubated at 15°C with 12 hours of alternating light and darkness. Germination was determined as the emergence of the radicle from the seed coat.

Soil seed longevity

To investigate the longevity of the soil-stored seed bank, a seed burial retrieval experiment was conducted at Site 1. Seeds were collected in late spring 2004 and divided into 20 lots of 10 seeds. Each seed lot was placed into a 10 x 10 cm free-draining nylon mesh bag filled with 50 grams of coarse river sand and sealed. In November 2004, a 3 x 3 m grid was marked with wooden pegs at four points. Bags were randomly selected and five bags buried 5 cm deep at each of the four points. These points were assigned to treatment by burial for 3, 6, 9 or 12 months. On retrieval at the end of the designated period, the five bags were assessed for numbers of decayed, germinated and intact seeds. Intact seeds were assumed viable and assessed for germination under controlled conditions as previously described.

Seedling emergence and survival in response to fire, smoke and raking

In May 2001, a limited number of 2 m x 2 m study quadrats were established at Site 1 to determine the effect of disturbance (fire, smoke application, raking and no disturbance) on seedling emergence and survival. Each of the 35 quadrats was centred on a single large mature plant of *G. maxwellii*. Five live and five dead plants were used in each of a control and two treatments (smoke and raking); five dead plants were used for the fire treatment with no live plants burnt. The minimum impact design for the disturbance experiment (that is, no live plants burnt) was adopted as a precaution due to the threatened nature of *G. maxwellii*. The canopy size (width of the canopy at the widest point and at 90° to the widest point) of each plant in the 35 experimental quadrats was measured prior to treatment. The mean canopy area of the plants assessed for each treatment was 1.03 ± 0.2 m^2 (fire), 0.8 ± 0.2 m^2 (smoke), 1.06 ± 0.2 m^2 (rake) and 1.1 ± 0.2 m^2 (control). In May 2001 five quadrats were subjected to a moderately hot autumn burn for roughly five minutes per quadrat. Prior to ignition an area of approximately 1 m around each quadrat was raked free of litter and plants to minimise the encroachment of fire on the surrounding bushland. Six ignition points were lit per quadrat. Each quadrat was assessed to have sustained between 95 – 99 % burn with flame heights varying between 0.5 m and 1.5 m high. Ten quadrats (five dead and five live plants) were treated with an aqueous smoke solution (Regen 2000®) at 100 ml m^{-2}. Smoke treated quadrats were pre-treated with a soil wettener (Wettasoil^{HG} by Garden King) at 5 ml m^{-2} to ensure even penetration of the smoke solution. Ten quadrats (five dead and five live plants) were hand raked to bare mineral soil using a rake hoe. Controls were left untreated. Seedling emergence was recorded in spring 2002 and biannually thereafter until winter 2006. All germinated seedlings in 2002 and subsequent years were tagged, numbered and plant growth measured annually. In the burnt quadrats, the mean seedling to parent ratio in the first spring after fire was calculated and the time to first flowering (primary juvenile period) recorded.

Natural seedling emergence and survival

In November 2001, five 5 m x 5 m quadrats were established at Site 2 where seedlings had germinated apparently in response to the unusually high summer rainfall of January 2000. Quadrats contained recently or long dead plants with the exception of quadrats 1 and 2 which each contained two live plants. Each seedling was identified with a metal tag, numbered and measured. Quadrats were monitored biannually until winter 2006. New seedlings in subsequent years were also tagged and numbered. Herbivore exclusion cages were erected around approximately half of all seedlings that emerged in August 2003 to determine the effect of grazing on seedling growth and survival. Plant growth and survival was recorded annually and the primary juvenile period recorded.

Data analysis

Seed production was estimated as the product of the number of inflorescent buds divided by the proportion of maturing fruit. From this data the percentage fruit set was calculated. Germination level has been expressed as a percentage of the number of intact seeds germinated. Time to first germination was recorded in days. Non-normal data were analysed using a non-parametric Kruskal-Wallis test to compare the percentage survival of fire-recruited seedlings at Site 1 to that of non-fire related recruitment at Site 2 (Statistica for Windows 1995. Statsoft Inc: Oklahoma).

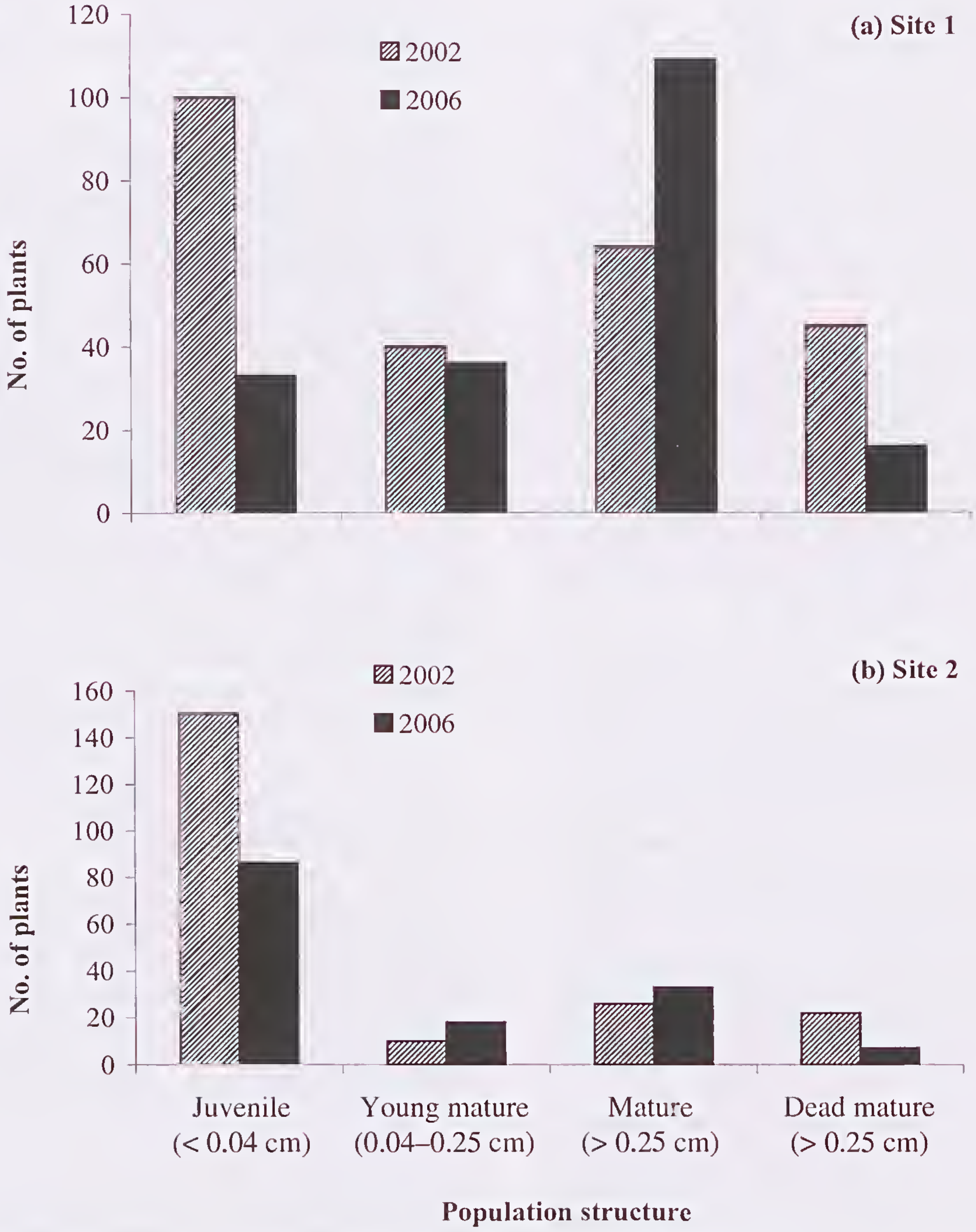


Figure 1. Population structure of *Grevillea maxwellii* at (a) Site 1 and (b) Site 2 in 2002 and 2006.

Results

Population structure

At the beginning of the study, the population structure at both sites showed a bimodal distribution with more large mature and juveniles plants and relatively few young mature plants present (Fig. 1a and 1b). Percentage mortality of mature plants was high with 30.2% of mature plants dead at Site 1 and 37.9 % dead at Site 2. At the end of the study both populations had increased in size with a 39.4 % increase in all mature plants at Site 1 and a 41.7 % increase at Site 2, while percentage mortality was 9.9 % and 12.1% at Site 1 and Site 2, respectively.

Fruit to flower ratio

A mean fruit to flower ratio of 0.0123 was recorded over one season at Site 1. High levels of fruit abortion were observed on all plants as well as high levels of seed predation.

Soil Seed bank

A total of 22 whole seeds were recovered from 40 soil samples at Site 1 giving a mean seed density of 24.4 ± 17.1 seeds m^{-2}. The soil stored seed reserve was not distributed evenly with four seed found beneath two live plants and 18 seed found beneath two dead plants. No seeds were retrieved from beneath plants at Site 2. A few samples contained seed fragments and shrivelled seeds indicating that a proportion of the seed crop was either predated and/or aborted. Full germination was attained for all retrieved soil-stored seeds. First germination commenced at 10 days with final germination achieved after 44 days (Fig. 2).

Soil seed longevity

A high proportion of seeds remained intact over the 12-month period of the experiment and ranged from 80 % after nine month's burial to 90 % after 12 month's burial (Table 2). Similarly, percentage germination of retrieved seeds remained high from the first retrieval at three months to the last retrieval after one year with the exception of the nine-month retrieval where percentage germination dropped to 65 %. Time to first germination for soil-stored seeds ranged from 11 to 15 days.

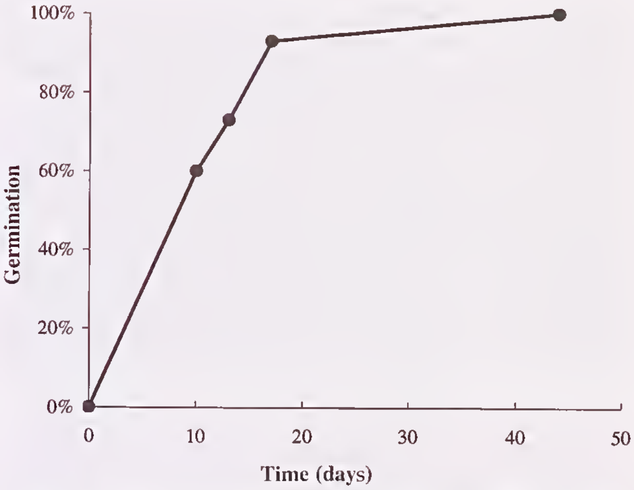


Figure 2. Percent germination over time in days of seeds retrieved from the soil seed bank of *Grevillea maxwellii* at Site 1.

Germination response and plant survival with and without disturbance

Total seedling emergence over the study period at Site 1 in 2 m^2 plots varied with treatment and ranged from six seedlings (no treatment) to 48 seedlings (fire treatment). Fire resulted in the greatest germination response with the highest seedling density of 1.9 m^{-2} recorded the first spring after the autumn burn at Site 1 (Table 3). There was a mean seedling to parent ratio of 9:1 in burnt quadrats. Germination continued the

Table 2

Percentage of *Grevillea maxwellii* seeds remaining intact after burial for 3, 6, 9 and 12 months at Site 1 and their percentage germination after pre-treatment with smoked water and manual scarification. N = 50 seeds retrieved at each time period.

Retrieval time in months	Percent seed remaining intact after burial	Percent germination of intact retrieved seeds	Time to first germination in days
3	86 ± 0.04	95 ± 0.05	11
6	82 ± 0.08	90 ± 0.08	15
9	80 ± 0.05	65 ± 0.10	15
12	90 ± 0.08	90 ± 0.04	14

Table 3

Mean density of seedlings (m^{-2}) recorded annually (not cumulative) in quadrats with disturbance (Site 1 only) and without disturbance (Site 1 and Site 2).

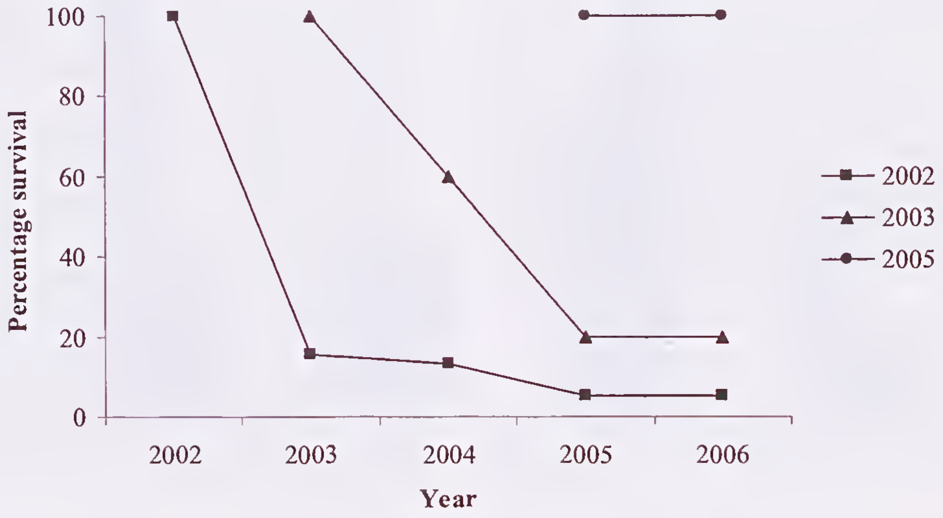
	Fire	Smoke	Rake	Natural (Site 1)	Natural (Site 2)
2000/2001	n/a	n/a	n/a	n/a	0.92 ± 0.19
2002	1.90 ± 0.17	0.13 ± 0.04	0.00 ± 0.00	0.00	0.04 ± 0.01
2003	0.25 ± 0.10	0.10 ± 0.06	0.03 ± 0.03	0.00	0.23 ± 0.13
2004	0.00	0.00	0.00	0.00	0.02 ± 0.02
2005	0.25 ± 0.08	0.18 ± 0.08	0.35 ± 0.13	0.15 ± 0.08	1.00 ± 0.43

subsequent and fourth year in the burnt quadrats but at much lower densities of 0.25 seedlings m^{-2}. There were very low levels of recruitment in response to smoked water and raking from 2002 to 2004. However, there was significant germination in 2005 in the raked quadrats. There was no natural recruitment recorded within control quadrats at Site 1 from 2002 to 2004 although low levels of germination were noted throughout the population. In contrast, high levels of germination were recorded at Site 2 (no disturbance) in 2001 and 2005, resulting in the next highest seedling densities recorded during the study of 0.9 m^{-2} and 1 m^{-2}, respectively. Total seedling emergence over five 5 m^2 plots at Site 2 for the study period was 276.

The overall survival of fire-recruited seedlings at Site 1 was low, with a mean survival of only 5.3 % in 2006 for the largest (2002) cohort (Fig. 3a). There was a higher percentage survival at Site 2 compared with Site 1 with 8.7 % of the largest (2000/2001) cohort surviving in 2006, however this difference was not statistically significant. By 2006, there were no survivors of 2002, 2003 and 2004 cohorts at Site 2 with steep increases in mortality recorded in the early years after germination (Fig. 3b).

Survival of seedlings over the first summer ranged from 15.8 % in 2003 to 100 % in 2006 at Site 1, and from 46.1 % in 2002 to 68.8 % in 2006 at Site 2. In the first summer after germination, 86.7 % of live and 39.1 % of dead seedlings of the 2002 (fire) cohort showed signs of grazing at Site 1. In contrast, only 7 % of the 2005 cohort (including raked, smoked and control quadrats) showed evidence of grazing. At Site 2, 36.4 % of live and 27.7 % of dead plants were grazed in the summer of 2002. As for Site 1, there was minimal grazing of the 2005 cohort in the summer of 2006. Of the 14 germinated seedlings of the 2003 cohort that were caged at Site 2 in August 2003, 12 were alive in summer 2004 while nine of 12 non-caged

(a) Site 1



(b) Site 2

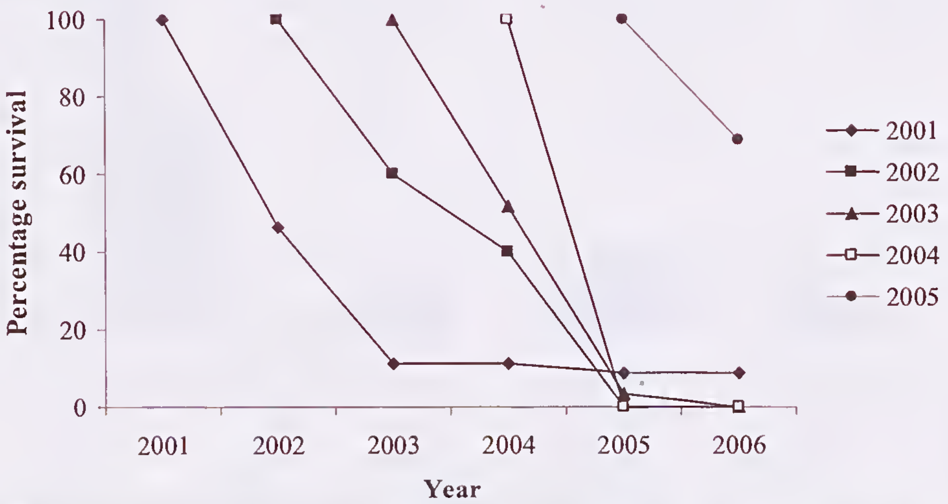


Figure 3. Percentage survival of successive cohorts of seedlings germinated over 4–5 years at (a) Site 1 (fire disturbance only); (b) Site 2.

plants survived. Mean plant height doubled from 2.5 cm to 5.0 cm for caged plants and by 2.0 cm from 2.4 cm to 4.4 cm for non-caged plants. However, by 2006, all of the caged and non-caged plants had died. Overall survival of all seedlings recorded over the study period, excluding the 2005 cohort, was 5.7 % at Site 1 and 6.6 % at Site 2.

The mean annual rainfall for the study period 2000 to 2006 was 411.9 mm, marginally less than the long term average of 420.5 mm (1968–2006). Below-average rainfall occurred in 2000, 2002, and 2004, with above-average rainfall in the three other years, with some significant peaks in rainfall in December 2001 (113 mm), August 2003 (133 mm) and March 2005 (147 mm). Over the study period, germination of *G. maxwellii* was observed primarily in the months of May and June and significant germination followed high rainfall between March and May 2005 (280 mm in total). The high rainfall events of December 2001 or August 2003 did not promote germination.

Juvenile Period

At Site 1, one of the two plants surviving of the 2002 cohort flowered in winter 2006, four years after germination. At Site 2, six of 13 surviving plants flowered in 2004, fours years after germination. This suggests a juvenile period of at least four years for *G. maxwellii*. Mean plant height at that time was 21.0 ± 2.0 cm and mean canopy dimensions were 44.3 ± 6.1 x 30.3 ± 5.2 cm. All of 10 surviving plants (8.9 % of the 2000 cohort) were reproductive in 2006, six years after germination.

Discussion

Successful recruitment and survival of perennial shrubs may be dependant on their reproductive biology, establishment ecology or a combination of both (Yates & Ladd 2004). Population stability relies on a balance between recruitment and mortality. In the present study, high levels of adult mortality of *Grevillea maxwellii* (30.2 to 37.9 %) were recorded at the onset in long unburnt (> 25 years) populations and this was suggestive of drought-induced mortality, death through senescence or a combination of both. Similarly, high levels of mortality and senescence were recorded for the rare re-seeder *G. barkylana* in a 29-year-old population (Vaughton 1998). Mortality of adult plants of re-seeder species may increase with time since fire and may be exacerbated by drought (Vaughton 1998). High levels of adult mortality have also been recorded for *G. calyei* in relation to fire history (Auld & Scott 2004). While significant numbers of small juvenile plants were observed at the onset of the present study it appeared that few of these survived to become young adults. However, by the end of the study both populations had effectively increased in size indicating that a proportion of juveniles were indeed successful in reaching maturity and that the seed bank continued to contribute to population dynamics either with or without disturbance stimuli.

Members of the Proteaceae have extremely low mature fruit to flower ratios compared to other temperate, hermaphroditic woody perennials (Collins & Rebelo 1987). Low fruit to flower ratios in *Grevillea* result from a combination of pollen limitation and high levels of flower and fruit predation (Hermanutz *et al.* 1998). The fruit to flower ratio of 0.0123 recorded in the present study was consistent with those of other members of the genus where ratios ranged from a minimum of 0.001 for *G. barklyana* (Vaughton 1998) to a maximum of 0.09 recorded for *G. oleoides* (Hermanutz *et al.* 1998). Low fruit to flower ratio in *G. maxwellii* may have resulted from high levels of abortion or inefficient pollination as well as pre-dispersal predation by insects and birds. The fragmented nature of *G. maxwellii* populations may influence the abundance and effectiveness of pollinators and therefore levels of abortion, but specific pollination studies would be required to confirm this. As no bird pollinators were observed over the study period, mammals are the more probable vectors.

Despite low annual seed production, *G. maxwellii* maintained a small highly viable but very patchy soil-stored seed reserve at one site. Edwards & Whelan (1995) also reported the presence of a small soil-stored seed bank for the re-seeder *G. barkylana*, with mean seed densities estimated at between 4.3 – 14.1 seeds m^{-2} from under-canopy samples. Seed bank size was related to time since fire and no seeds were retrieved from outside the canopy area of the plants studied. Although these seed densities are somewhat smaller than those reported during the present study for Site 1 (24.4 seeds m^{-2}), there was considerable variation between samples and many had no seed at all which is comparable with our results for *G. maxwellii*. Seed bank densities from 0 to 30 seeds m^{-2} were recorded for the re-seeder *G. rudis* while no seed bank was detected for the rare resprouter, *G. althoferorum* (Burne *et al.* 2003). In contrast, soil seed bank density in the present study was considerably lower than that recorded for *G. rivularis* (194 seeds m^{-2}) a species which occupies habitat subject to periodic disturbance from both fire and flood (Pickup *et al.* 2003).

Data from the seed burial experiment indicates that the soil seed bank of *G. maxwellii* persists in a highly viable state for at least one year. The seed bank of the rare *G. calyei* was estimated to have a half-life of 7.6 years (Auld *et al.* 2000) remaining in the soil for many years after the death of adult plants. Recruitment of *G. maxwellii* seedlings under dead plants suggests seeds may also remain viable in the soil for several years after the parent plant dies and are available for recruitment when an appropriate stimulus is provided. Unfortunately, there is little in the literature regarding the ability of species with soil seed banks to maintain a seed bank after fire (Auld & Denham 2006). The ability to maintain a soil-stored seed bank may buffer the impact of high frequency fires. If some residual seeds remains in the soil there will be some risk spreading at least in the short-term, providing species with a second chance at recruitment. The present study showed that although the density of seedlings was considerably lower in the second and fourth years after fire, a small viable seed bank had persisted over time. The persistence of a soil seed bank after fire has also been reported for the threatened Proteaceous species *Persoonia micranthera* and the weakly serotinous *Dryandra ionthocarpa* subsp. *ionthocarpa* (Barrett unpublished data). The persistence of a residual soil seed bank may be related to depth of soil burial. Where seed dormancy in *Grevillea* species is broken by a combination of smoke and heat shock it has been suggested that the smoke cue may decline with soil depth (Auld & Denham 2006).

Despite the establishment of few plots and restricted treatments in accordance with a minimal impact design experiment for threatened species, fire at Site 1 provided the most successful experimental disturbance stimulus for seedling emergence of *G. maxwellii*. Fire regimes play an important part in the ecology and survival of many plant species in fire-prone environments. Recruitment is frequently linked to fire and obligate seeding species are often dependent on recruitment after fire or other disturbance for persistence in the landscape. Heat associated with fires is an important mechanism for releasing dormancy (Fenner & Thompson 2005) and the role of heat in the induction of seed germination of many Western Australia fire-following plant species is well documented (for example see Bell *et al.* 1993; Bell 1999). Heat acts to fracture the seed coat of hard-seeded and other species (Bewley & Black 1994). Smoke has also been shown to increase stimulation of germination in species from Mediterranean fire-prone environments (for example see Brown & van Staden 1997; Keeley & Fotheringham 1998; Roche *et al.* 1998), although Bell (1999) noted that a number of studies reported that smoke-induced seed germination was less successful than heat in the induction of germination. In the present study, the results indicate that smoke treatment did not stimulate germination of the soil-stored seed to the same degree as heat from fire, and few seedlings emerged in quadrats treated with smoke and none of these survived summer drought conditions. Similarly, there was little recruitment in direct response to raking. Although smoke treatment was used in the laboratory to stimulate germination of fresh and aged seeds, no seeds were germinated under non-smoke treated conditions for comparison due to a lack of available seeds. However, significant germination in the absence of disturbance was observed in 2001 and 2005. Recruitment in 2005 in particular appears to have been triggered by high rainfall in March of that year. While fire-related germination cues are most common in the genus *Grevillea* (Kenny 2000, Morris 2000), episodic recruitment after disturbance other than fire has been reported in a number of species including *G. longifolia* (Auld 1995), *G. buxifolia* and *G. speciosa* (Auld & Tozer 1995), *G. caleyi* (Auld & Scott 1996), *G. macleayana* (Vaughton 1998) and *G. rivularis* (Pickup *et al.* 2003). Seedling recruitment in *G. rivularis* has been recorded after fire, flood and mechanical disturbance with seeds showing marked dormancy polymorphism with 36 % of soil-stored seeds germinating without treatment. Thus the species can respond to disturbance by fire or flood. The results of the present study clearly indicate that seeds of *G. maxwellii* can also respond to non-fire related cues such as the episodic rainfall events previously described and we suggest that seeds may be polymorphic. Polymorphism has been reported also for *G. barklyana* (Edwards & Whelan 1995) who suggest that decreased dependence on fire as a means of germination stimulation may be associated with increased fire interval. Seed age and weathering over time may play a role also in a recruitment event with wetting and drying cycles over summer and autumn contributing to the release of any seed dormancy. It is possible that summer rainfall events may have depleted the seed bank at Site 2 through recent recruitment, thus accounting for lack of a discernable soil-stored seed reserve.

The seedling to parent ratio of 9:1 and seedling density of 1.9 m^{-2} recorded in the present study for *G. maxwellii* is lower than that of 20:1 and 4.6 m^{-2}, respectively, recorded for *G. barklyana* (Vaughton 1998). However, recruitment in the latter species was negligible in the absence of fire and this species is likely to be more fire-responsive than *G. maxwellii*. Furthermore, only dead plants were burnt in the present study, and there may have been greater recruitment from burning living plants.

High levels of seedling mortality were a feature of both sites in the present study. Early seedling mortality is a widespread occurrence in woody plants (Harper 1977). Lack of adequate moisture is often a controlling factor that limits survival, and where seedling densities are high, mortality can increase (Clarke 2002). Survival curves for seedlings of semi-arid shrubs are approximately 1 % (Clarke 2002). Survival of the two major cohorts followed in the study ranged from 5.3 to 8.7 % and overall 5.7 % and 6.6 % of all germinated seedlings survived at Site 1 and Site 2, respectively. In contrast, 90 % survival was recorded for fire-recruited seedlings of *G. barklyana* over a 2-year period (Vaughton 1998). However, the latter study coincided with two years of above average rainfall demonstrating the importance of adequate soil moisture for seedling survival. In contrast, the 2002 rainfall in the present study was 130 mm below the average which would have had a significant impact on post-fire establishment and seedling survival. Grazing can also have a profound effect on seedling survival (Clarke 2002) and loss of seedlings at both sites in the present study was partially attributed to herbivore grazing. Defoliation of many seedlings resulted in suppressed growth, possibly increasing the juvenile period. The prime factor that contributed to low seedling survival after recruitment is not clear. Herbivore grazing or drought conditions or a combination of these factors may have been responsible. However, drought was probably the more significant factor in seedling mortality as several seemingly dead and grazed seedlings recovered following winter rains while no caged seedlings survived the study period. Grazing was largely restricted to the summer period with little or no grazing noted over winter and spring. The major decline in seedling numbers occurred during summer and seedling death during this time is attributed to below average rainfall following recruitment. At Site 1, 86.7 % of live and 39.1 % of recently dead, fire-recruited seedlings exhibited signs of grazing. This was considerably higher than at Site 2 where 36.4 % of live and 27.7 % of dead plants had been grazed in unburnt vegetation.

Seedling recruitment between fires may be strongly related to the availability of competition-free sites in addition to rainfall (Yates & Ladd 2004), and the relatively high level of recruitment in the raked quadrats in 2005 suggests that germination of *G. maxwellii* under adequate soil moisture conditions may also be dependent on the presence of adequate gaps in the canopy.

While flowering commenced in the present study at fours years after germination, peak flower and fruit production may take many more years. Flowering of *G. barkleyana* occurs after 2 to 3 years, although maximum inflorescence and fruit production did not occur until 15–

16 years after fire when plants reached full size but declined thereafter (Vaughton 1998). The juvenile periods of other obligate seeding *Grevillea* species (*G. caleyi* and *G. longifolia*) (Vaughton 1998) are comparable to that of *G. maxwellii,* although in contrast, *G. wickhamii* had not flowered four years post-fire and only one third of *G. dryandri* plants had flowered after three years (Williams *et al.* 2006).

Conclusions

Although constrained by a limited number of plots and treatments in accordance with a minimum impact design experiment, this study has provided a temporal insight into the ecology and population demography of *G. maxwellii.* We have identified that the two populations studied are not in decline, at least in the short term. However, the long term success of the inter-fire recruitment documented in the present study is unclear. This study suggests that factors associated with the availability of the regeneration niche may be more important than reproductive factors, and population persistence may be more related to stochastic environmental events (Yates & Ladd 2004). Small fragmented populations of *G. maxwellii* are highly vulnerable to stochastic events such as wildfire followed by drought conditions. Climate change may increase the risk of wild-fire and create adverse conditions for seedling survival potentially causing local extinctions of *G. maxwellii.*

While it is possible that summer rainfall events may become more frequent in the south-west of Western Australia (CSIRO 2001), the overall projected decline in annual rainfall may limit the numbers of seedlings that survive to maturity. There may be some risk spreading through the maintenance of a residual seed reserve but recruitment will be dependent on the magnitude of the germination cues as well as the location of seeds in the soil profile (Auld & Denham 2006). Infrequent disturbance can also cause local extinction, particularly in small isolated fragments as adult plants senesce (Keith 1996; Yates & Ladd 2004). The soil seed bank may buffer loss of genetic diversity in small populations through i) its ability to increase effective population size to well above that of the adult plants, ii) by the longevity of the seed bank enabling storage of genetic diversity long after adult plants have died and iii) through the presence of multiple generations of seeds in the seed bank due to some remaining after fire (Llorens 2003). However, the seed bank buffering powers may be limited and are unlikely to prevent the loss of genetic diversity in populations that remain small over several generations causing inbred individuals that may have lower fitness (Llorens 2003).

Future investigations aimed at quantifying predation and removal rates of *G. maxwellii* seeds would provide useful data to assist in understanding the relationship between seed production, soil seed bank size and recruitment. Quantification of the soil-stored seed reserve over time would permit a greater insight into the dynamics of the seed bank. Population modelling may assist in predicting population dynamics over a range of environmental conditions however the soil-stored seed reserve needs to be considered in estimates of population abundance where there is a high level of senescence and death of above-ground plants (Auld & Scott 2004). It is critical that *G. maxwellii* populations are managed to ensure that entire populations and / or multiple populations do not burn in a single wild-fire event. Controlled burns targeting small portions of these long unburnt populations may reduce the impact of potentially high post-fire seedling mortality. With anticipated warming climates, the future persistence of *G. maxwellii* in the wild is in doubt. Little can be done to counter the effects of a warming climate and the influence this will have on seedling survival.

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Detection of phytoplasma in *Allocasuarina fraseriana* and *Acacia saligna* in Kings Park

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Abstract

Phytoplasma-like symptoms which included bunchy growth, witches' broom and 'little leaf' were observed in *Allocasurina fraseriana* (Western Sheoak, Casuarina) and *Acacia saligna* (Acacia, Orange Wattle) trees in Kings Park and Botanic Garden. The affected trees were in a poor state of health or appeared to be dying. Many trees of other species exhibited similar symptoms. A sensitive, diagnostic method based on the polymerase chain reaction (PCR) was used to detect the presence of phytoplasma in symptomatic and asymptomatic leaf and root samples from the trees. The amplified PCR products were sequenced and the sequences submitted to Genbank as Casuarina (accession number EF474451) and Acacia (accession number EF474452). Sequence analysis indicated that the phytoplasma detected in plants belonged to the 16Sr II group and was closely related to *Candidatus* phytoplasma aurantifolia. Phytoplasma-associated disease has therefore been confirmed for the first time in casuarina and acacia trees in Western Australia.

Keywords: Western Sheoak, *Casuarina*, Acacia, Orange wattle, Common Wattle, *Candidatus* phytoplasma aurantifolia

Introduction

Phytoplasmas are phloem-limited plant pathogens of the class *Mollicutes*. Symptoms of phytoplasma-associated disease vary between host plant species and also the types of phytoplasma. Infection may be characterised by stunted growth, reduced leaf size, little leaf, witches' broom, leaf deformation, hardened stems, leaf and stem discolouration, sterility, phyllody, virescence or gigantism, dieback, and big bud (Davis *et al.* 1997; Lee & Gundersen-Rindal 2000). In recent studies phytoplasma-associated diseases have been identified in Western Australia (WA) affecting several host species including chickpea, tomato, snakebean, paddymelon, sweet potato, clovers and Paulownia trees (Davis *et al.* 1997; Bayliss *et al.* 2005; Saqib *et al.* 2005; 2006a; 2006b; Tiaro *et al.* 2006), although the identity of plant species that act as reservoirs for phytoplasmas that affect crop species is not known.

A. fraseriana (Western Sheoak or Casuarina) is native to WA and grows in the region between Perth and Albany. *A. saligna* (Orange wattle, Common wattle) is also native to the southwest region of WA. Many of the casuarina and acacia trees in Kings Park and Botanic Gardens showed symptoms of witches' broom, stunted growth, dying back of branches and small leaves. Confirmation of the presence of phytoplasma disease associated with these trees in WA is lacking although a phytoplasma-associated disease was reported in *Allocasurina muelleriana* in South Australia (Gibb *et al.* 2003).

Phytoplasma in plants can be identified using the polymerase chain reaction (PCR) by amplification of the 16S rRNA genes with RFLP analysis of the product to differentiate 'clades', and nested PCR can be used to increase the sensitivity of the assay (Streten & Gibb 2006). The differences in sequences of 16S rRNA genes helps to differentiate members of the phytoplasma clade into at least 15 groups (Lee & Gundersen-Rindal 2000; IRPCM Phytoplasma/Spiroplasma Working Team–Phytoplasma Taxonomy Group 2004). Nested PCR and subsequent DNA sequence analysis has been used to confirm the presence of phytoplasma disease in symptomatic casuarina and acacia trees in Kings Park and Botanic Garden, Perth.

Methods

Leaf and root samples were collected in Kings Park and Botanic Garden from both symptomatic and asymptomatic trees of *A. saligna* and *A. fraseriana* in September 2006 with further samples collected in July 2007. Because uninfected control plants could not be found in Kings Park, further leaf and root samples of the two species were collected from the Banksia Reserve, Murdoch University, South Street campus in August 2007. The affected plants were selected based on the presence of symptoms such as witches' broom, stunted growth, little leaf and controls samples were collected that had no visible symptoms. Root and leaf samples from two symptomatic *A. saligna* trees and four symptomatic *A. fraseriana* trees from Kings Park were analysed. The *A. fraseriana* and *A. saligna* trees with severe witches' broom structures had roots that appeared to be growing normally. Similarly root and leaf samples from two asymptomatic trees each of *A. saligna* and *A. fraseriana* were collected from Kings Park and Banksia Reserve at Murdoch University as negative controls. All

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root samples were washed twice with deionised water to remove adhering soil and debris, followed by rinsing with 100% ethanol then 70% ethanol. The samples were stored overnight at 4°C in plastic bags before DNA extraction.

The hot cetyltrimethylammonium bromide (CTAB) method was used to extract DNA from 1g of the leaf and root tissue samples separately (Dellaporta *et al.* 1983; Zhang *et al.* 1998). The first round of PCR was done using primers P1 and P7 followed by a second round using internal primers R16mR1 and R16mF2 (Deng & Hiruki 1991). The PCR conditions were as described in Saqib *et al.* 2006b. The nested PCR products (~1400bp) were then analysed by electrophoresis on a 1% agarose gel. A previously cloned 16S rRNA gene of Sweet Potato Little Leaf (SPLL) phytoplasma isolated from snakebean GenBank (accession no DQ375777) was used as a PCR positive control (Saqib *et al.* 2006b).

The ~1400bp PCR product was sequenced directly from both ends using Big Dye Terminator 3.1 (Perkin-Elmer, Foster City, CA), with an Applied Biosystems 3730 DNA capillary sequencer. The nested PCR products were sequenced using 3.2 picomole of primer R16mR1 and R16mF2. Two different PCR products from each sample of leaves and roots were sequenced to check for the possibility of mixed infection with different phytoplasmas and to prevent errors in editing. The 16S rRNA gene sequences were analysed using BioEdit™ version 7.0.5.3 software.

Results

The symptoms of disease-affected *A. fraseriana* and *A. saligna* trees were consistent wherever they occurred in Kings Park. The majority of symptomatic trees appeared to be dying or were already dead. The most common symptoms observed were witches' broom, stunted growth, little leaf and dying back of the branches (Fig. 1 & 2). Nested PCR analysis of the *A. fraseriana* and *A. saligna* samples confirmed the presence of phytoplasma. The phytoplasma infections were identified in all symptomatic leaf and some root samples (Fig. 3). One root sample from symptomatic *A. saligna* and three root samples from symptomatic *A. fraseriana* were negative for phytoplasma infection whilst leaf samples from the same plants were positive for phytoplasma-associated disease. All of the samples from asymptomatic plants of both species collected specifically as negative controls in Kings Park were also found to contain phytoplasmas (Fig. 4). PCR controls and absence of diagnostic bands in source samples showed that this was not a result of experimental contamination. As a result of this observation asymptomatic samples of *A. fraseriana* and *A. saligna* from Murdoch University were also analysed. In this case clear negative controls were obtained of both species, except in one root sample from *A. fraseriana* (Fig. 5).

The 1400 bp regions between primers R16mR1 and R16mF2 (corresponding to the16S rRNA gene) from both *A. fraseriana* and *A. saligna* plants were sequenced. Sequences from *A. fraseriana* and *A. saligna* root and leaf samples were 100% homologous. Partial sequence data from symptomatic and asymptomatic *A. fraseriana*

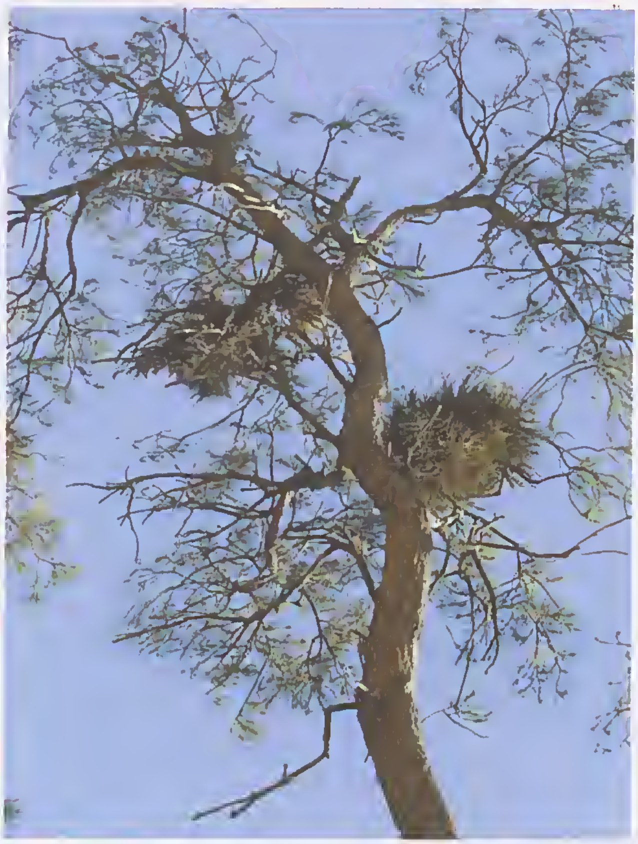

Figure 1. Diseased *A. fraseriana* tree in Kings Park (September, 2006). Many leaves and branches were dead or dying, but the bunchy growths with little leaves and multiple stunted shoots are clearly visible.

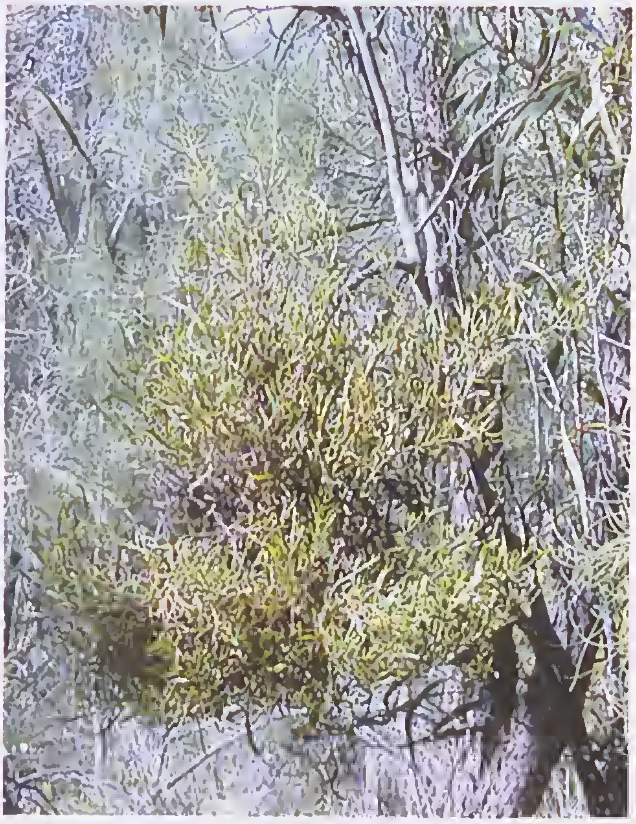

Figure 2. Diseased *A. saligna* tree in Kings Park with phytoplasma-like symptoms such as little leaf, stunted bushy growth, and witches' broom (September, 2006).

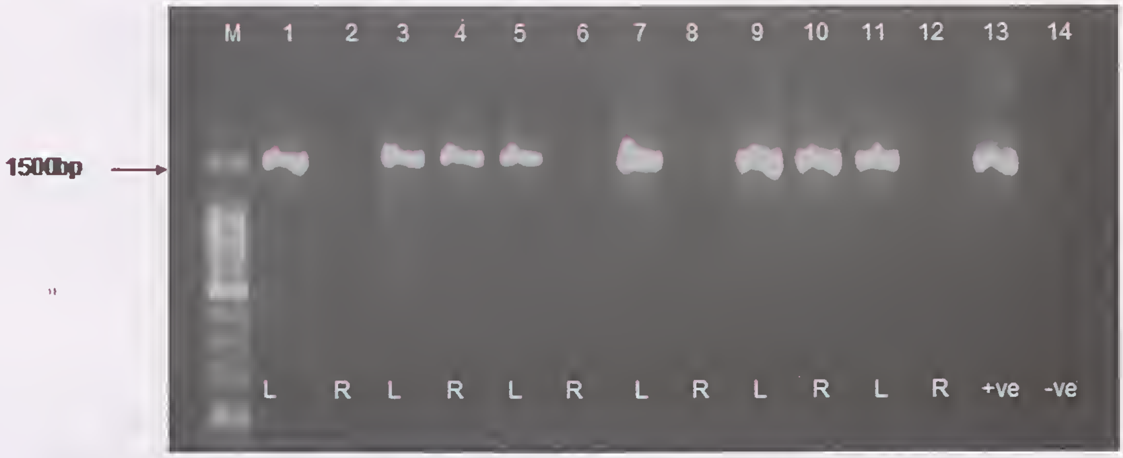
M 1 2 3 4 5 6 7 8 9 10 11 12 13 14
1500bp
L R L R L R L R L R L R +ve -ve

Figure 3. 1% agarose gel showing PCR products amplified from sample tissues collected from Kings Park and Botanic Garden. M = 100bp ladder (Promega). L = Leaf tissue. R = Root tissue. Lanes 1-4, *A. saligna*: Lanes 5-12, *A. fraseriana*: Lane 13, PCR positive control (SPLL): Lane 14, PCR negative control.

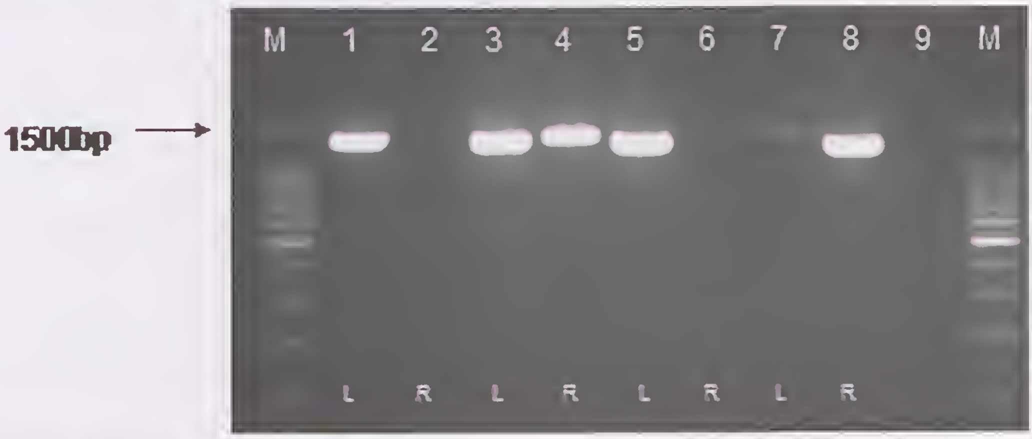

Figure 4. 1% agarose gel showing PCR products amplified from asymptomatic sample tissues collected from Kings Park and Botanic Garden. M = 100bp ladder (Promega). L = Leaf tissue. R = Root tissue. Lanes 1-4, *A. saligna*: Lanes 5-8, *A. fraseriana*: Lane 9, PCR negative control.

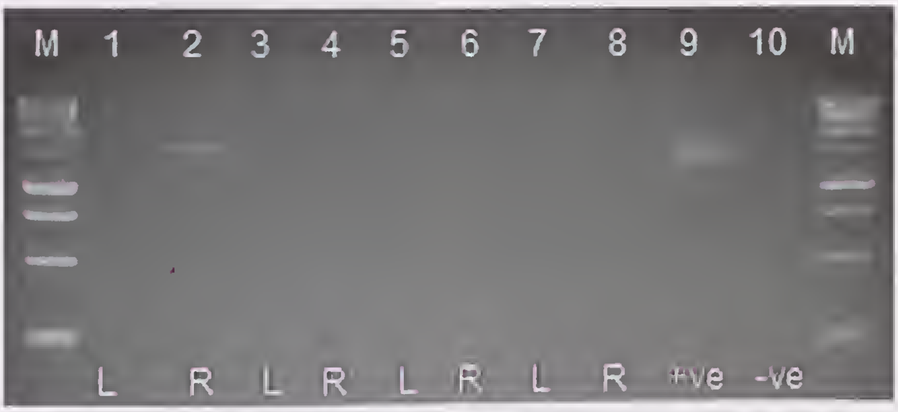

Figure 5. 1% agarose gel showing PCR products amplified from asymptomatic tree samples collected from the Banksia Reserve, Murdoch University. M = 1Kb ladder (Promega). L = Leaf tissue. R = Root tissue. Lanes 1-4, *A. fraseriana*: Lanes 5-8, *A. saligna*: Lane 9, PCR positive control: Lane 10, PCR negative control.

roots and leaves were reported as one sequence and 1368 bases were submitted in GenBank (accession no EF474451). Similarly partial sequences from *A. saligna* were compared and combined as one sequence and 1362 bases were submitted to GenBank (accession no EF474452). Partial sequence data of 1353 bases from asymptomatic *A. fraseriana* roots from the Banksia Reserve, Murdoch University were also submitted in GenBank (accession no EU095022). A BLASTN search of the NCBI (databasehttp://www.ncbi.nlm.nih.gov/BLAST/Blast) was carried out to identify homology with other phytoplasma sequences. The sequences from *A. fraseriana* and *A. saligna* were 100% homologous to the 16S rRNA gene of Sweet Potato Little Leaf (SPLL) GenBank (accession no AJ289193) belonging to *Candidatus* Phytoplasma aurantifolia (16Sr II, strain V4).

Discussion

Many individuals of *A. fraseriana* and *A. saligna* in King's Park and Botanic Garden appeared unhealthy and exhibited symptoms of witches' broom. These two tree species are prominent in the park and their disfigurement detracts from its aesthetic value. This study was undertaken to seek to identify if phytoplasma disease was an underlying cause of these symptoms. The results of analysis of rRNA genes from DNA extracted from affected tree samples showed the presence of phytoplasmas in all symptomatic trees sampled. Furthermore, the asymptomatic plants collected specifically as negative controls also tested positive either in leaf or root samples or in both. This suggests that the majority of these species of trees in Kings Park are affected with phytoplasma. To obtain clear negative control results, it was necessary to analyse additional asymptomatic samples from a separate site (Murdoch University campus), and even at this site one plant of *A. fraseriana* showed presence of phytoplasma. Based on the sequences of the amplified DNA the phytoplasma present was identified as identical to that of Sweet Potato Little Leaf which belongs to *Candidatus* Phytoplasma aurantifolia (16Sr II). To our knowledge this is the first report of phytoplasma affecting casuarina and acacia trees in WA.

It is possible that other trees and shrubs that display similar symptoms may also be affected by phytoplasmas. It is also possible that other factors, such as lowering of the water table or infection with other pathogens could contribute to the diseased state of the trees in Kings Park. Although phytoplasma-associated disease has been identified in various plant hosts in WA (Bayliss *et al.* 2005; Saqib *et al.* 2006b; Tiaro *et al.* 2006) there is very little information on the extent of phytoplasma infection on other native species or insect vectors and the mode of transmission of phytoplasmas. The insects which have been shown to be vectors of phytoplasma-associated disease (Pilkington *et al.* 2004) and which are also present in WA include leafhoppers (*Membracoidea*), plant hoppers (*Fulgoroidea*) and psyllids (*Psylloidea*).

There are a number of reports of phytoplasma disease in WA in a range of cultivated and native plants (Doepal 1964; Goss 1964; Padovan *et al.* 2000; Saqib *et al.* 2005; 2006a), and it is likely that native plants act as reservoirs of phytoplasmas, from which infection of commercial plants can originate (Saqib *et al.* 2005; Bayliss *et al.* 2005). Plants that appear to be affected by phytoplasma can be found readily in most regions of WA including the Kimberley (Saqib *et al.* 2005), the Southwest (Bayliss *et al.* 2005; Saqib *et al.* 2006a) and Gascoyne region (Saqib *et al.* unpublished). The occurrence of phytoplasma disease in WA remains largely unmonitored and in general this disease has been ignored, so that there is little effort specifically to prevent spread of phytoplasma disease either to native bushland or to crop plants from native reservoirs. This is a subject which requires further research, particularly on vectors and the mode of transmission, understanding the host-pathogen interaction and additional factors that contribute to the diseased state.

Kings Park is culturally significant to Perth, as well as being a valuable source of tourism revenue to the state. To preserve its attractiveness and minimise damage to trees associated with phytoplasma disease, management action, such as control of insect vectors and removal of affected trees could be taken to prevent further spread.

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'Green above, paler below': descriptions in the literature of the colour in trees from southwest Australia

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Abstract

This paper outlines descriptions of colour in the literature pertaining to the flora of the South-western Australian Floristic Region, comparing pre-settlement exploration by Dutch, French and English voyagers with modern general texts. It was found that colour has been and continues to be poorly described, preventing any analysis of the biological diversity of colour to enable comparison across or between floras or species. Forthcoming work on more accurate colour description using the Natural Color System of Sweden is foreshadowed.

Keywords: Colour description, botanical history, south-western Australia

Introduction

This paper is a specific survey of how colour has been described in the literature and in early exploration in south-western Australia. This study arose from questions regarding the changing colours of the landscape due to extensive urban development in south-western Western Australia, within a centre of world biodiversity. Perth, Western Australia, has one of the fastest growing urban sprawls in Australia and, while most studies or analyses of urban sprawl on the world scale refer to sprawl as moving into farmland, this is not the case in Western Australia, where expansion is primarily into bushland. Indeed, Seddon (1995) described Perth as 'a city in the bush', whether coastal heath or banksia-eucalypt woodland. Perth's bushland also lies within one of only five Mediterranean-type ecosystems in the world (Beard *et al* 2000), the South-western Australian Floristic Region, and is a designated Global Hot Spot of Biodiversity (Myers *et al* 2000; Hopper & Gioia 2004).

Trees were the major focus of the colour survey described here as tall trees have dominated the conservation debate in Australia for more than a century (Bonyhady 2000, Griffiths 1996, 2002) and trees are most missing from new residential subdivisions in south-western Australia (Farrelly 2003). In newer subdivisions clear-felling or strip-clearing is common. With increasing urbanisation, and in-fill housing of older suburban areas, endemic trees which survived older suburb creation are likely to be lost. Farrelly (2003) found that exotic species comprised more than 86% of new plantings in new suburbs in south-western Australia. With the loss or impoverishment of larger endemic trees in suburbia, and their extensive replacement with exotics, whether from outside Australia or from other regions within Australia, are the colours of Australian flora being lost at the regional level?

Colour is an aspect of biological diversity not addressed previously, although with suburban development and changes of species in suburban Australia the colours and textures of vegetation are changing. Yet the colours particular to Australia have long been part of the national psyche, as much as the 'emerald' of Ireland and the 'green and pleasant land' of England. For the indigenous people of south-western Australia, the region remains the land of the Rainbow Serpent - a Dreamtime spirit who brought the gift of colour to the world (Nannup, pers.comm.). Settler poets and storytellers, who have fashioned feelings towards Australia both within and without the country, have written famously of the "*sunburnt country*" (Mackellar 1907), with its "*vision splendid of the sunlit plains extended*" (Paterson 1895), and that "*this is the land of colour, burning colour*" (Ingamells 1951), with "*million-coloured*" gumtrees (Ingamells 1945).

Early descriptions of Australian trees are those by natural historians and botanists. It was enticing to ask if plant colour was remarked upon, and how, and how tree colour was recorded historically. Thus this first paper on colour is a specific historical literature survey and focuses on tree colour described in early accounts and then in currently existing scientific, educational, and general texts on the flora of south-western Australia. The jump from historic to present has been used as a method of quickly assessing any change in accuracy in two hundred years, or any attempt at a methodology of colour description towards more detail and precision in more recent years. This paper can be seen to be the first stage in a study which seeks to examine and codify colour description in one part of a flora. A forthcoming paper will describe the colours of leaves and trunks of tree species in south-western Australia, using the Natural Color System of Sweden and colour methodology developed by Anter (1996) and these will later be compared with non-endemic species planted in the region.

Methods

Two main methods were used in the study, a search of early historical colour descriptions of trees in the landscape, and a literature search of currently available works on trees from southwest Australia. This is based on asking how trees were first seen by explorers, botanists, and artists, and how they are currently described in the botanical literature. References were taken from readily obtainable published sources only, and no systematic search has been made of ephemera and unpublished journals or notes.

Trees selected for this study emphasised the Myrtaceae as it contains the most conspicuous and characteristic group of Australian trees, particularly in the sub-family Leptospermoideae which includes *Eucalyptus*, the most important genus of Australian trees, and *Melaleuca*. Melaleuca's very name is from the Greek *melas* (black, dark) plus *leucon* (white); it is believed that the first species described had white papery bark with a stocking of burnt trunk (Boland *et al* 1984).

The study went beyond the range of trees within the immediate metropolitan region of Perth, in order to gain greater insight into the manner in which Australian trees are described, but does restrict itself to those species most common, visible, or famous in southwest Australia. Additionally included were some eastern states endemics that are widely planted in Perth as street trees or as replacements for south west endemics in parks. In some cases 'colourful' trees have been selected deliberately as a comparison with what might be construed as 'plainer' trees, and the grass tree, the monocot *Xanthorrhoea preissii*, is included in this list as it has been increasingly used as a 'designer tree' in the southwest by landscape architects and other garden designers. Species were grouped alphabetically, and not in plant associations, which are complex.

With regard to historical accounts by naturalists and explorers well before the establishment of the first settlement in southwest Australia at Albany in 1826, any description of colour of any part of the flora in the southwest of Australia was sought, and comments also noted about the general colour of the wider southwest landscape. In the course of this study comments regarding the eastern seaboard made, for example, by Banks, Solander, and Cook in 1770, were excluded in order to confine this investigation to a manageable scale and with a south-western focus. A small number of additional contemporary comments from early settlers were included.

Modern texts readily available to the public were searched for descriptions of the colour of the parts of tree species in south-western Australia. Books and other sources were selected and confined to those available from bookshops, academic or otherwise, and major libraries. Journals were excluded on the basis that it is likely that more general texts are based on these. FloraBase (1995), an on-line government compendium, was also consulted.

The colours of juvenile leaves, mature leaves, stems, trunk and bark, flowers, and fruits were recorded. Particular attention was paid to leaf colour and to bark/trunk. The seasonal differences in bark and trunk are especially important in gum-barked (smooth-barked) eucalypts, where the bark is annually deciduous and with shedding of the old bark, the new inner bark (the new layer of functional tissue) is exposed, and this is often highly coloured (Boland *et al* 1984). Seed colour, though described in some detail for some species, for example in the banksias by George (1981), was not listed, as the purpose of this study is not to capture colour in hidden parts but is confined to those parts readily visible in the landscape. As such, it is focused on the inherent colour (Anter 1996) of easily visible parts. Inherent colour is the colour taken from a close distance, and was chosen for this study as the examination of plant parts by botanical taxonomists is done at this distance. This is in contrast to perceived colour, which is that impression given by distance (Anter 1996). It should be noted, however, that in many historical references it is difficult to separate inherent and perceived colour.

It is not unusual for plant common names to celebrate some aspect of their colour and this study also collates some of the major tree species of the south-west that have a common name which reflects in some way the colour of the species, most usually the colour of flowers or trunk.

History of Colour Descriptions

Beginnings

This is regarded as a colourful land. The southwest of Australia is the land of the Rainbow Serpent, known as the *waakarl* in Nyoongar, who shed tears, and the rainbow, onto the southwest. The land of the Nyoongar corresponds to that of the West Australian Christmas tree, *Nuytsia floribunda* (related by Len Collard, Nyoongar elder, Conference: *Water: histories, cultures, ecologies*. University of Western Australia, July 2003), a highly distinctive orange-flowered tree, called *mooja* in Nyoongar, and considered by Beard (1990) to be one of the great flowering trees of the world. The Nyoongar seasons are six, that of late winter and early spring being *djilba*, the season of yellow, when *Acacia* species are in flower, and it is the gold and green of acacias that was to be taken up by newer Australians as the country's national colours. This is the season that the poet Dorothea Mackellar would describe as "golden-green…clear-shining after rain". Generally, indigenous Australian languages do not contain many colour words, but usually name colours by the name of the thing which has that colour – for example, while *djilba* is a colour word for yellow-green, it is primarily the word for grass, and *djilba* is the season of grass (Dench, pers.com.). Indeed, it was suggested by Moore (1884) that the word marri (*Corymbia calophylla*) was taken to be the tree by European settlers, but it is also the Nyoongar word for blood, from its red kino.

Early visitors

While the Dutch ship the *Duyfken* is believed to be the first European ship to sight and also record the Australian coast in 1606 (Wood 1969), and the Dutch were sighting the treacherous western coast and suffering from its dangers on their route to Batavia throughout the seventeenth century, it was not the Dutch who made the first recordings of floral colour in Western Australia. William Dampier visited the north-western coast in the *Cygnet* in 1688, publishing the account. In this work (Dampier 1697) he described a bloodwood tree, probably *Eucalyptus dampieri* (George 1999), with "*Leaves are of a dark colour*" and "*the Rind is blackish*", and noted the colour and taste of the exuded gum to be like the dragon tree (*Dracaena draco*) of the Canaries. Though regarded as a buccaneer, Dampier was a natural historian, kept detailed and accurate records, and was experienced and skilled in collecting and pressing plant specimens, stating that knowledge "*was the main thing I regarded*" (George 1999).

The Dutch, who had no naturalists on board, were business-motivated, and were searching primarily for precious metals, vegetables, spices, elephants, and Kingdoms, following the Dutch saying of the time that 'Jesus Christ is good, but trade is better' (Edwards 1989). Hence Dutch records give nautical information, some general landscape description of topography as reference points for the sailor, and comments on the aridity of the southern landscape, but little detailed botanical description. Perhaps the very first surviving description of colour in the south-western Australian flora by a European is that made during Willem de Vlamingh's voyage to South Land (the west coast of Australia discovered in 1616 by Dirk Hartog). The upper surgeon Madrop Torst[1], records in his diary on the 12th January 1697, at a landing along Perth's Swan River, that "*several of these trees yielded a kind of resin, almost like lacquer, brownish-red in colour*" (Schilder 1985); this is clearly kino – defensive material produced by a healthy tree to deal with larval attack (Hadlington & Johnston 1977) - of a eucalypt, and is probably either the marri, *Corymbia calophylla*, or the tuart, *Eucalyptus gomphocephala*. Torst was a better recorder of what he saw than his captain Vlamingh (Appleyard & Manford 1979), who was reported by his fellow officer Witsen as often "*under the drink*" (letter cited in Schilder 1985, p. 215). Unfortunately, Torst ate the seeds of the zamia palm, *Macrozamia riedlei*, which are highly toxic (Isaacs 1987) and was so violently ill for the rest of the exploration party's trek inland that he wrote little else about what he saw. The nuts of zamia were seen by early explorers in the camps of Aboriginals, and they presumed that they were edible, but the explorers did not understand that the indigenous people had been employing a complicated process to remove the toxins from the nuts, with archaeological evidence for this process for at least 14,000 years (Smith 1993).

Although two professional artists were engaged for Vlamingh's voyage in order to "*paint whatever curiosity they encounter*" (Schilder 1985), we have no recording of close descriptions of plants, the artist Victor Victorszoon making mostly watercolour sketches of the western coast, with distant sheens of green or blue-green coastal heath, and noting hills and sand-dunes. However, plants were collected, as two specimens are housed in the Geneva Botanic Garden (Sharr 1988; Gooding 1991; citations in Richards 1997, p.6).

A year after Vlamingh, in August 1699, Dampier was back on the northern coast of New Holland in the *Roebuck*, and recorded in his journal (Dampier 1703) a "*large sort of Sampier, which bears a white Flower*" and further noted thick bushes "*full of Leaves; which were mostly long and narrow. The Colour of the Leaves was on one Side whitish, and on the other Green; and the Bark of the Trees was generally of the same Colour with the Leaves, of a pale green. Some of these Trees were sweet-scented, and reddish within the Bark, like Sassafras, but redder. Most of the Trees and Shrubs had at this Time either Blossoms of Berries on them. The Blossoms of the different sort of Trees were of several Colours, as Red, White, Yellow, Etc., but mostly Blue...*". These observations were published in his work *A Voyage to New Holland* in 1703. The blue flowers which predominated on the coast were probably of *Dampiera incana, Sceavola holosericea* and *S. crassifolia* (Hopper 2003). During this voyage, Dampier also recorded "*blue and yellow flowers*" and a flower of "a *deep red colour*" thought by George (1999) to be the Sturt Pea, *Swainsona formosa*, which was flowering at that time of the year. Dampier's interest and close annotation of colour, which contrasts with later voyages by others, might well have derived from his experiences in 1675 along the mangrove swamps of the Mosquito Coast in the Caribbean. Following the earlier suppression of piracy by the English in the Caribbean, many buccaneers such as Dampier turned their attention to the gathering of logwood, *Haematoxylon campechianum*, which was used in Europe for the making of black dye (Finlay 2002). There, Dampier noted in his journals the colours of the cut tree, and the colouration of the dye – an interest which was revealed in his colour descriptions in Australia.

Talented professional artists were found in the later scientific expeditions of the French and English. Drawings of both flora and fauna were made during expeditions along the south-western coast during the voyages of George Vancouver (1791), Antoine-Raymond-Joseph Bruni D'Entrecasteaux (1792), Nicolas Baudin (1801–3), Matthew Flinders (1801–1802, 1803), Louis Desaules de Freycinet (1818), Jonathon King (1801–02), and Dumont D'Urville (1826). All may reveal a little more of the European's first forays into the nuances of south-western Australia's botanical colour. St Alouarn (1772) passed by the southwest coast near cape Leeuwin, but did not land until Shark Bay (Godard & de Kerros 2002).

During Vancouver's scientific expedition inland in 1791 the botanist Archibald Menzies, accompanied by Captain Vancouver, commented on plants in full bloom, and that they traversed "*groves of trees hills and valleys forming a rich and picturesque prospect boldly drawn by nature's manly pencil*" (Menzies 1791). Menzies' journal of his visit to King George Sound, Albany, in 1791 gives no report of colour in plants, although he noted detailed colour in a snake. Like the Dutch before him, he noted a "*reddish gum*" produced by a eucalypt, and the "*marks of fire around their bottoms*", but gave no other written detail of colour although he was clearly delighted by the "*beautiful groves of evergreens*" (Menzies 1791).

In 1792 the naturalist Jacques Julien Houtou de Labillardière was a member of the expedition of Bruni D'Entrecasteaux which was searching for the lost scientific expedition of La Pérouse in the ships *Recherche* and *L'Espérance*. [Note: La Pérouse and his expedition died in the Santa Cruz group in the Pacific. Their failure to return to France caused great consternation. Louis XVI was an active sponsor of French maritime exploration, and collaborated in plans for the expedition of both La Pérouse and D'Entrecasteaux, and was regarded as having added New Holland to the list of geographical priorities to La Pérouse's voyage; his favourite subject was geography (Horner 1995). The wreck was discovered in 1827 by an Irish sealer and confirmed by Dumont D'Urville in 1828 (Marchant 1998, Horner 1995)].

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[1] Mandrop Torst was upper-surgeon on the hooker-ship, *Nyptangh*, which sailed with the ship, the *Geelvinck*, and the galliot, the *Wezel*, which comprised Vlamingh's fleet. Vlamingh skippered the *Geelvinck*.

Like Menzies the year before, Labillardière was also clearly enthused and enchanted by much of the country he saw, both in 'Cape Diemen' (Tasmania) and south-western Australia. He writes often of the beautiful plants, gathering *"a beautiful species of leptospermum, remarkable for its silvery leaves, and its flowers of bright red"* (Labillardière 1800, Volume i. p.426; see Horner 1995). Notations of plant colour are rare in his account, however, and this is curious as he describes much more readily the colours of animals, and even records "flies of a fawn colour" (Labillardière 1800, Volume i, p.175). This may be simply because Nicholas Piron, the artist on board, was to draw the plant specimen, or some specimens, while Labillardière was conscientious in his description of plant structure. The emphasis on plant structure can be understood as botanists at the time were very much absorbed with the classification of their new riches, and this is fundamentally based on sexual parts as outlined in 1753 by Linnaeus in *Species Plantarum*. To describe without an emphasis on sexual structure has proved problematic. For example, Robert Brown's later treatments in 1810 and 1830 of all known *Banksia* still hold today except for those species in which he placed too great an emphasis on foliar characters (George 1981). Despite his Linnaean treatment, a few descriptions of plant colour do occur in Labillardière's journal. He found "*a beautiful plant*" which he designated *anigozanthus* (sic.), and, wrote that: *"The corolla presents the form of a tube, divided on its margins into six unequal parts, recurved inwardly; it is covered with reddish hairs"* (Labillardière 1800, Volume ii, p.441), *and noted that "the capsule is nearly spherical, and of the same colour as the flower by which it is surmounted…", and "the top of the stem is covered with reddish hairs, like the flower. I have called this species anigozanthus rufa."* This was the first kangaroo paw described. It's common name is Red Kangaroo Paw.

Green and yellow were earnestly captured by Piron in the botanical plate of *Eucalyptus cornuta*, the yate (see Marchant 1998). *Banksia repens* and *Banksia nivea*[2] were also found, and *B. repens* painted by Redouté (see Marchant 1998). Labillardière describes the former with "*a creeping stem, covered with a thick reddish down*", and *B. nivea* as "*remarkable on account of its long leaves, which are white underneath, and very deeply dentated.*"(Labillardière 1800,Volume ii, p 443–444). Labillardière was the first to describe *Nuytsia floribunda* (Dukyer 2003, p.134) although he did not see it in flower. The species was not recorded in his journal but in his publication *Nova Hollandiae plantarum specium* (1804–1807) (Duyker 2003) which recorded the vast number of botanical specimens collected by the scientists aboard D'Entrecasteaux's expedition. Banks, when examining the collection before it was returned to the National Assembly of France, found a vast herbarium of some ten thousand specimens a "*testimony of an industry all but indefatigable in the Botanists who were employed*" (cited in O'Brian 1987, p.254).

Expeditionary 'artists' were not always as well qualified as Piron to do the job. In Nicolas Baudin's expedition to Terre Australes of 1801–03 with the *Géographe*, Charles-Alexandre Lesueur was a petty officer and had only been appointed "sketcher" for the expedition with the desertion of the artist at the Île-de-France (Mauritius) en route to Australia (Marchant 1998) and likewise Nicholas Martin Petit was an assistant gunner employed as an artist by Baudin. In May 1801 Baudin sailed with Freycinet, Hamelin (who explored Rottnest Island in Baudin's consort the *Naturaliste*), Péron the anthropologist, Leschenault the botanist, Lesueur the gunner and artist, several scientists such as the zoologist Maugé, Riédlé the gardener, and Guichenot and Sautier the assistant gardeners. In May 1801 Baudin was to recount in his diary that sometimes during his voyage along the southwest coast of Australia "*we made out a few plateaux with trees of a rather lovely green, all of which only served to make looking at the parts that lacked them more disagreeable…*" (Baudin, 29 May 1801, p.162). Baudin himself did not describe much in the way of botany that is useful (Marchant 1998), and very little of colour, as he was more concerned with the safety of his men, nautical details, and the problems of running his ship and his often arrogant young officers (Fornasiero *et al* 2004). In an entry dated 31 May 1801 he records near Cape Leeuwin, that "*the most common tree is a type of eucalyptus which grows only moderately high. One also finds quantities of a shrub which grows in clumps. The shape and scent of its leaves are like those of the laurel, but Citizen Riedlé told me that it was a type of Phillyrea*" (possibly *Diplolaena dampieri*, Dampier's Rose; this is a shrub to 2 metres and has aromatic leaves, and is a member of the Family Rutaceae). *"Another tree furnished me with a type of gum, a sample of which I am giving you. Its leaves are rather similar to the vetiver"* (the grass, *Andropogon muricatus*) *"and form a bunch which sprouts on top of a fairly thick coal-coloured trunk"*. This last is *Xanthorrhoea preissii*, the balga. Baudin writes (Baudin, 23 February 1803): "*The botanists were very pleased with the collections that they made. From what he has told me, Citizen Leschenault appears to have gathered roughly two hundred new species of plants that were unknown to him and as many varieties within the species. Guichenot, the gardener, is no less satisfied and has even more specimens*". Yet few of them survived this expedition, for of the twenty-three scientists who left on the voyage, only three returned due to the ravages of dysentery and scurvy (Appleyard & Manford 1979, p. 100).

François Péron's journal was published with Louis Freycinet as *Voyage de découvertes aux Terres Australes.*

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[2] Excluded (George 1981), and now placed as *Dryandra nivea* (Labill.) R.Br., the couch honeypot. *Nivea* refers to its colour, 'snowy' (George 1984b), a reference to its leaves which are white underneath.

The first English language account of his notes regarding the south-west, published in 1809, is considered a very flawed translation and much scientific content was abridged or excluded (Duyker, pers. comm.). Baudin is regarded as a better anthropologist than Péron, who tended to give judgement and theorise without foundation (Fornasiero *et al* 2004). Nevertheless, Péron's most interesting discovery for the seeker of tree colour is of a place where he speculated during a solo walk after he had become separated from the rest of the party (Duyker 2006). Just north of the present-day regional city of Busselton, Péron found a highly-organised space which he styled a 'Garden temple' with twelve large trees which were *"white from the base of their trunk to the extremity of their branches*" (Wallace 1984, p. 46–47). Marchant (1998) took these to be paperbarks (*Melaleuca* species) since they were near the river, although Péron made no mention of the papery nature of the bark, and paperbarks would have been common, not distinctive, in this wetland region of meandering creeks and extensive seasonally wet palusplains. Tuart, *Eucalyptus gomphocephala,* is possibly the tree in question for, although not startlingly white to those familiar with the powderbark eucalypts, they were called 'white gum' by early settlers. Other possibilities relate to Nyoongar tradition. Noel Nannup, a Nyoongar elder, recalls that generations ago seed of jarrah, *E. marginata,* had been planted out of its range to 300km east near Kulin and grown at an important Dreaming Trail site (reported in Beresford *et al* 2001, p.31), and Péron's 'Garden temple' could be another instance of a species planted deliberately outside its range for ceremonial purposes by Nyoongar people. Thus these trees might have been *Eucalyptus laeliae* (though in May the trunk is likely to appear butter-yellow), the Darling Range Ghost gum, or one of the wandoos, *E. accedens,* the powderbark, or *E. wandoo,* wandoo. This site is known of to the Nyoongar people of Busselton as an important site but has been lost through extensive clearing for pastures.

During the Baudin expedition a party from the *Naturaliste* also landed on Carnac Island and reported many large trees, now gone, and plants with red and yellow flowers, which may have been *Eremophila glabra.* Although not found on Carnac Island today, this species is a palatable plant (Mitchell & Wilcox 1994) and might have been eaten out by rabbits introduced to the island by French or American whalers,in the 1820s (Rippey & Rowland 1995). The final comment about colour came when, at a site which the French took to be monuments to warriors, spears which had been daubed with red eucalyptus resin were found (Baudin 22 February 1803, p.486–487).

The French expedition of 1801 led by Baudin was engaged in charting the last missing sections of the Australian coastline and studying its natural history. At the same time, and in response to Napoleon's global ambitions, Captain Matthew Flinders of the Royal Navy was doing the same thing in the *Investigator.* Travelling with Flinders were the natural historians - the naturalist Robert Brown, the botanical illustrator Ferdinand Bauer, and the gardener Peter Good (Wege *et al* 2005). They collected plant specimens in King George Sound during the months of December 1801 and January 1802. The British expedition of Flinders, sailing west, famously met up with the French expedition of Baudin, sailing east, near Kangaroo Island in Encounter Bay in April 1802, and shared geographical information and the perils they had both encountered (Fornasiero *et al* 2004). It is not known if they commented on the botany they had both been collecting.

From the British expedition, Robert Brown published his *Prodromus florae Novae hollandiae et Insulae Van Diemen* from 1806 to 1816 and Bauer began to publish his *Illustrations Florae Novae Hollandiae* in 1813, but this work did not meet with sufficient encouragement for the volumes to be continued after the third number (Henrey 1975). Bauer is renowned for the accuracy and detail of his drawings, and was particular regarding colour (see Watts *et al* 1997). His method was to draw in pencil and code the colours according to a colour grid. For his Australian visit he employed a grid of almost 1,000 colours, giving him remarkable accuracy although the drawings were completed much later in London (Hewson 1999; Pignatti-Wikus *et al* 2000a, 2000b). An example of his colouring technique is given in the watercolour of Figure 1.

Although few are extant, the technique of employing a colour grid by botanical artists dates from the 16th century, and can be seen in those of Waller (1686) and Syme (1814) (Fig. 2). The use of grids by botanical and other artists fore-shadows the introduction in the twentieth century of colour grids and patches for colour analysis, such as the Munsell Color System (Munsell 1975), the Royal Horticultural Society, and the Natural Color System of Sweden (Agoston 1979). The extant codes of Brenner (1680) contains 30 colours, that of Waller (1686) contains 119 colours and that of Syme (1814) 108 colours. Bauer used three colour charts and that of his early years is discussed and displayed by Lack and Ibáñez (1997) (shown in Fig. 2), which is of a colour code of 140 colours. Bauer's later colour codes are seemingly lost, and were more extensive. In addition to a numerical code for hundreds of colours in his later codes, Bauer includes Roman numbers, and annotations on his pencilled sheets in both Latin and German, and there is the suggestion that Bauer used more than one colour code for each drawing. Many authors writing about Bauer have been concerned about his colour codes, as noted by Pignatti-Wikus *et al* (2000b). Hewson (1999) considers that Bauer's colour grid in Australia must have been exceptional in its size.

Pignatti-Wikus *et al* (2000a, 2000b) fully describe Bauer's field-drawings made in Australia in pencil and give the colour numbers from his grid. Further, they have outlined the structure of 994 colours and consider that the colour chart's colour sequence followed a combination of three fundamental colours – red, blue, and yellow – with white and black. In this collection, Bauer gives from between a few to three dozen colour numbers per plant, for various plant parts; leaf colour is rarely represented by only one number, even in these mostly shrubby plants collected. For example, in the small Trigger plant, *Stylidium adnatum* R.Br., Bauer notes five sequential numbers, bringing a comment from Pignatti-Wikus *et al* (2000a) regarding the subtlety of colour combinations given by the artist. Again, this level of discernment foreshadows the use of modern colour charts for colour description.

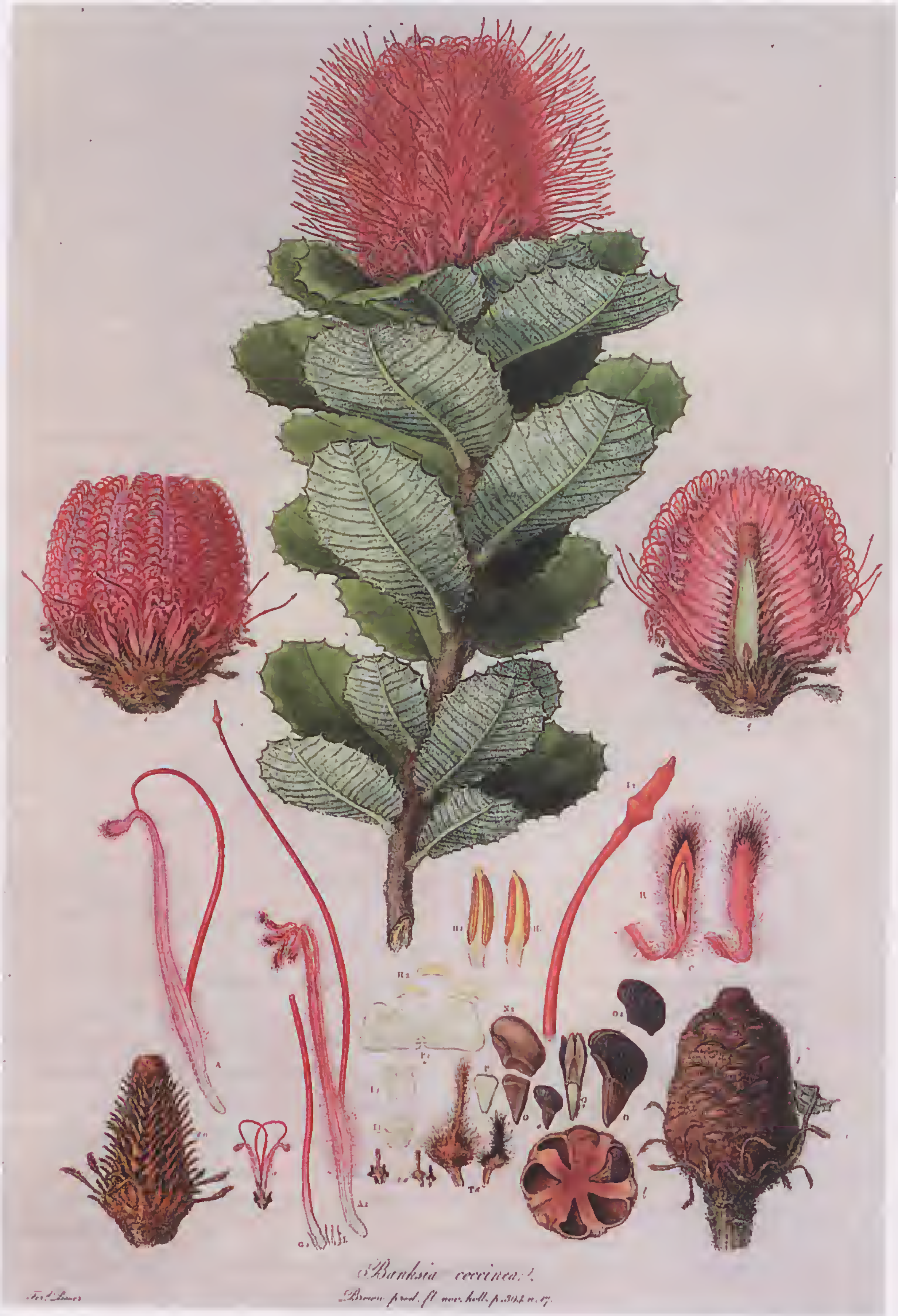

Banksia coccinea. !
Brown prod. fl. nov. holl. p. 394 n. 17.
Ferd. Bauer

Figure 1. *Banksia coccinea* drawn by Ferdinand Bauer from a specimen collected at King George Sound, Albany, on the south-western coast of Australia.

Few expeditions added botanical notes on colour after Bauer. Freycinet returned to western Australian waters again in 1818 in the *Uranie*. Newly married, his artist wife Rose Pinon had been smuggled aboard at Toulon, and sketched the party, who only visited Shark Bay, and recorded no information on colour. Baxter collected on land along the south coast east of Albany as far as Cape Arid in 1823–1825 but no records exist of colour description. Jules Dumont D'Urville in the man-o-war *Astrolabe* collected for eighteen days at King George Sound, during the months of October and November 1826, and carried an official artist, Louis de Sainson, who painted many scenes of the area. No precise botanical colour annotations were made by Sainson regarding colour but in one scene showing men on the Kalgan River, the yellowish smaller trees strongly suggest acacias, whether in flower or with new growth. Rosenthal (pers. comm.) notes the mixed abilities of early European painters to capture the colour and shapes of Australian trees. Further, he points out that while those who made pictures in the early colonial period in Australia were untalented amateurs, the Europeans were struggling at home with the colours and shapes of European trees as well, even amongst their most distinguished landscape artists (Rosenthal 1999). As in England, the problem in Australia seemed to be of mind, palette and technique, rather than any inaccurate reading of the bush. Indeed when viewing Gainsborough - who used broccoli as a prop for his paintings to represent trees (Rosenthal 1999) - in England and early colonial artists it could be claimed that the trees were painted in very much the same manner, with fluffy extrusions, and few could be identified as species or even genera wherever they were geographically located. An exception to this is the view of species given in a drawing by Lesueur in 1807 of the Empress Josephine's Paris Chateau, Malmaison, which was planted with *Casuarina*, *Acacia*, and *Grevillia* under the direction of Péron, and members of these genera can be made out in the view, given in Wallace (1984) because they are depicted correctly regarding the shape of their canopy.

Early settlers

The site of Albany on the south coast was settled in 1826. In 1827 Captain James Stirling of the *Success* travelled by ship's boat up the Swan River, where Perth was settled in 1829, as far as Upper Swan, now a growing area of urbanism amóngst vineyard country which had been established shortly after settlement. Charles Fraser accompanied Stirling and his glowing report, in which he referred to "*trees clothed in the richest green*" was a major impetus to British settlement. Hopper (2004) gives an outline of post-settlement collections by natural historians. Of note are the reports of Baron Karl von Huegel from his visit in 1833–34 in which he enthused on the great variety of colour in the flora. Huegel noted the same change in colour between the view when perceived at a distance to that of inherent colour when perceived close-up as analysed and described by Anter (1996). Huegel wrote that when viewed close-up "*the cheerless grey-green*" seen at a distance "*changed to the most vivid hues, mingled with brilliant flowers of every kind, in untold numbers...I roamed around this world of colour as if intoxicated*" (Clark 1994).

Once settlement occurred many setters began to annotate colour in the new vegetation around them, as did Charles Darwin who commented on the "*bright green colour of the brushwood*" in his visit in 1836 (Sellick 1997). While a full critique of the enticing question of the early white settlers' responses to the colours of Australia's flora is outside the scope of this paper, some comments can be made of the very earliest settlers. Jane Dodds, an early pioneer who arrived in Swan River colony on the *Rockingham* in 1830, recorded "*dark green trees*" from the boat, with the country near Guildford, upriver from Perth, "*exceedingly beautiful*", with shrubbing trees, "*the bloom of one being a rich bright orange*", another "*a bright lemon*", and a third "*rich crimson tipped with white*" (Heal 1988, pp 31 and 45). These describe *Nuytsia floribunda*, possibly *Melaleuca polygaloides*, and *Banksia menziesii*. Mrs E. Millet (Millet 1872), the wife of the Anglican minister at York, 60km east of Perth, noted that "*The white trunks of some of the trees were so much flecked with dark-brown spots*" (probably *Eucalyptus wandoo*)... "*and ... I saw a lizard spotted brown and white, precisely in the same manner as the trees; I therefore concluded that it was* of a *sort that lived amongst them, and was shielded by its colour from the notice both of its enemies and of its own prey.*"

Settlers began to give common names for the new species in the south-west, many of which have survived today. Many common names reflect colour, whether of bark, leaves or flower, and Table 1 gives tree species whose common name employs colour. Some species have two names, the indigenous and the European; in some cases the original European appellation has been largely forgotten and the indigenous name applies in common parlance today. Though it is arguably leaf colour that reflects more than anything the colour which trees impart to their greater environment, bark colour seemed particularly important in perception of the colour of trees; this appears to be especially true of the larger species and perhaps reflects the human viewpoint from the ground. Colour plays a role in keying out plants species in field guides, as shown in keys given in Brooker & Kleinig (2001) for the eucalypts. For example, adult leaf colour is used to separate *E. marginata* into subsp. *marginata* and subsp. *thalassica*. There are other examples where 'adult leaves discolorous' is used to key out from 'adult leaves concolorous'.

Table 2 gives a short representative descriptive range, taken from thirty species examined, of tree species in south-western Australia to indicate the different ways in which colour is described today in existing literature and the issues which arise in colour description. These types of description remain the basis of colour discussion in the taxonomic and general literature on flora. Descriptions distinguish leaves as either dark or light, and if the adaxial and abaxial are different; they compare one species with another in the same genera—for example, *Eucalyptus todtiana* is considered to have leaves of a "paler green" than the other eucalypts of the coastal plain (Seddon 1972), but it does not elucidate which green; descriptions indicate, but do not give, a range of colours and they reveal a desire to convey a range of colour, such as the "white to light brownish" bark of *Melaleuca preissiana*, (Boland *et al* 1984). There is

Table 1

Tree species of southwest Australia with a common name reflecting a colour feature of bark, trunk or leaf; sources are various and combined. Indigenous names are given where known. Note that some indigenous names are very site-specific. Primary sources for indigenous names of the south-west Nyoongar are given in Abbott (1983), Moore (1884), or personal communication from Maher[3]. Bennett (1991) gives a recommended name where there is more than one for a species.

Tree species	Specific name	Refers to	Indigenous name if known
Acacia cyclops	Red-eyed wattle, Coastal wattle	Seed; Not seen from afar but when pods open red seed	n/a
A. saligna	Black wattle Orange wattle	Red-orange bark	*Cujong*
Banksia attenuata	Candle banksia, Coast banksia	Bright yellow inflorescences	*Biara* and the flower *mangyt* (Moore 1884, p.91, 101); Piara (Abbott 1983)
B. coccinea	Scarlet banksia	Red inflorescence	n/a
B. grandis	Bull banksia; many banksia species around Australia were early termed 'honeysuckle'.	'Bull' possibly from indigenous name of *bulgalla/boolgalla*; 'Honeysuckle' from sweet-tasting substance in flowering cone (Moore 1884, pgs.91 & 136)	*Poolgarla, mangite, beera, boolgalla, boorarup* (Abbott 1983; Daw *et al* 1997, p.40); Flowers soaked in water produced a sweet drink known as *mangite* or *mungitch* (Daw *et al* 1997, p.40).
Corymbia calophylla	Marri, red gum	Marri has copious quantities of kino, which is red when fresh and hardens/ congeals to a darker mark on tree	*Marri, Gardan, Nandap* (Abbott 1983, p.19); Mari is the Nyoongar word for red blood (Maher, pers. comm.).
C. ficifolia	Red-flowering gum	clusters of red to orange flowers	n/a
C. haematoxylon	Mountain marri	Greek *haemat,* blood-red, referring to the heartwood	n/a
Dryandra sessilis	Parrotbush	Attracts colourful birdlife, namely ring-neck parrots, black white-tailed cockatoos, New Holland honey eaters, for nectar or seed	*Pudjak, Budjan, Butyak,* (Abbott 1983)
Eucalyptus accedens	Powderbark	White 'dust' on trunk which is powdery	n/a
E. albida	White-leaved mallee	Juvenile leaves; Latin *albida,* somewhat white. Bark also white	n/a
E. arachnaea	Black-stemmed mallee	Dark grey to grey black bark	n/a
E. argyphae	Silver mallet	Trunk and bark, especially when wet or in moonlight	n/a
E. astringens	Brown mallet	Smooth coppery brown trunk with brown shedding bark	*Malard, Mallat*
E. caesia	Gungurru	Latin *caesius* means 'bluish-grey' refers to leaves	*Gungurru*
E. camaldulensis	Red gum, River gum, River red gum	Bark colours	*Itara, Piipalya* (Bennett 1991)
E. campaspe	Silver topped gimlet	Youngest branchlets grey to almost white	n/a
E. carnei	Carne's blackbutt	Dark bark near the ground	n/a
E. clivicola	Green mallet	Blue-green leaves	n/a
E. crucis	Silver mallee	Silver -grey young branches and branchlets	n/a
E. cylindriflora	White mallee	Trunk	n/a
E. decipiens	Moit, Red heart	Wood	*Moit*
E. dissimulata	Red-capped mallee	Operculum bright red near flowering	n/a
E. diversicolor	Karri	Many-coloured trunk	*Karri*
E. erythrocorys	Red-cap gum	Scarlet bud cap; Greek *erythros* meaning red	*Illyarrie*
E. erythronema	Red-flowered mallee White mallee, white-barked mallee	Flowers red, pink or white; trunk powdery white; Bark varies from intense white to purplish-red	n/a

Table 1 (cont.)

Tree species	Specific name	Refers to	Indigenous name if known
E. falcata	Silver mallet	Trunk is silver	*Dulyumuk, Toolyumuck*
E. flavida	Yellow-flowered mallee	Pale yellow flowers	n/a
E. foecunda	Slender-leaved white mallee	White bark	n/a
E. gardneri	Blue mallet, blue-leaved mallet	Adult leaves	*Kwoakol*
E. gomphocephala	Tuart, White gum by some European settlers.	Trunk appears grey; Salvado refers to the wood as being white and extremely hard (Salvado 1977, p. 212). White gum seems odd name except at some conditions of light, particularly in the larger trees in summer, and in trees seasons after fire; but big trees and burning uncommon in the metropolitan area now	*Duart*
E. gracilis	Red mallee, white mallee	Red-brown bark in late summer, or grey bark at base; seedling stems red	*Yorell??*
E. griffithsii	Griffith's grey gum	Bark in older trees	n/a
E. guilfoylei	Yellow tingle	Trunk colour	*Dingle Dingle*
E. jacksonii	Red tingle	Bark grey over red brown	n/a
E. kondininensis	Kondinin blackbutt or black yate	Dark bark on lower trunk	n/a
E. laeliae	Butter gum or Darling Range Ghost gum	Bark pure white or creamy yellow/butter yellow in autumn; Moore (1884,p. 135) refers to a white or blue gum with bark of a light slate-colour and smooth bark; he noted that some on high ground have a tinge of a rusty colour mixed with French white. [French white is finely textured powder]	Possibly *Nelarak*
E. lane-poolei	Salmon white gum	Trunk	n/a
E. longicornis	Red morrel	Trunk	*Moril*
E. macrocarpa	Mottlecah, blue bush	Leaves and young branchlets powdery grey	*Mudelka*
E. marginata	Jarrah; called Swan River mahogany by first white settlers.	Mahogany from red wood	*Djara* a general term for bush (Maher, pers. comm.) (The 'djar' sounds as in the little bottle)
E. marginata subsp. *thalassica*	Blue-leaved jarrah	Bluish leaves	n/a
E. melanoxylon	Black morrel	Bark is black-grey	n/a
E. nutans	Red-flowered moort	Flowers red or creamy white	n/a
E. ornata	Silver mallet	Light grey or silvery smooth trunk	n/a
E. patens	Yarri, blackbutt	Bark dark at foot	Dwuda
E. pluricaulis subsp. *porphyrea*	Purple-leaved mallee	Prominent purplish leaves in the crown	n/a
E. pyriformis	Dowerin Rose	Large bright flowers	
E. redunca	Black marlock	Trunk; known also as black-barked marlock	n/a
E. rhodantha	Rose mallee	Brilliant red flowers	
E. rudis	Blue gum, Flooded gum, Swamp gum	Leaves	Kulurda (Abbott 1983)
E. sepulcralis	Blue weeping gum	Youngest branchlets grey-red	n/a
E. stoatei	Scarlet pear gum	Red flower buds	n/a

Table 1 (cont.)

Tree species	Specific name	Refers to	Indigenous name if known
E. salmonophloia	Salmon gum	Bark is smooth and white to silver-grey in winter but salmon pink to coppery in summer and autumn; name is from Latin *salmoneus* (salmon-coloured) and Greek *phloios* (bark)	*Wurak*
E. tetragona	Tallerack, White marlock, silver marlock, white-leaved marlock	Branches are white; Beard (1990, p.141) notes that the tallerack is conspicuous throughout its range and its blue-green foliage give a dominant character to the vegetation.	*Dalyeruk*
E. todtiana	Coastal Blackbutt or Prickly bark	Black feet	n/a
E. torquata	Coral gum	Pink flowers	n/a
E. transcontinentalis	Redwood	Red-brown wood	*Pungul*
E. wandoo	Wandoo, white gum	White bark; In mature trees the discolouration of the bark is an indication of tree hollows containing water (Daw *et al* 1997, p.32)	*Wandoo, wawnt*
E. woodwardii	Lemon-flowered mallee	Bright lemon-yellow flowers	n/a
Nuytsia floribunda	WA Christmas tree; originally cabbage tree by first white settlers.	Brightly coloured at Christmas and weeks preceding	*Moodjah/mungah, mudja;* Particularly known that the spirit of a dead person goes into this tree; is a women's area, often for birthing. Men not allowed at sites with these trees (Maher, pers. comm.). Moore (1884, p.55) notes that it was "very abundant" on the Swan Coastal Plain.
Xanthorrhoea preissii	Blackboy, Balga	Appearance of aboriginal with spear to settlers	*Balga* or *Palga* for whole plant; also *ballak, galgoyl, yango, tdudtin* (Moore 1884, p.118); leaves *mindar*, inflorescence *waljap* (Moore 1884, p.118).

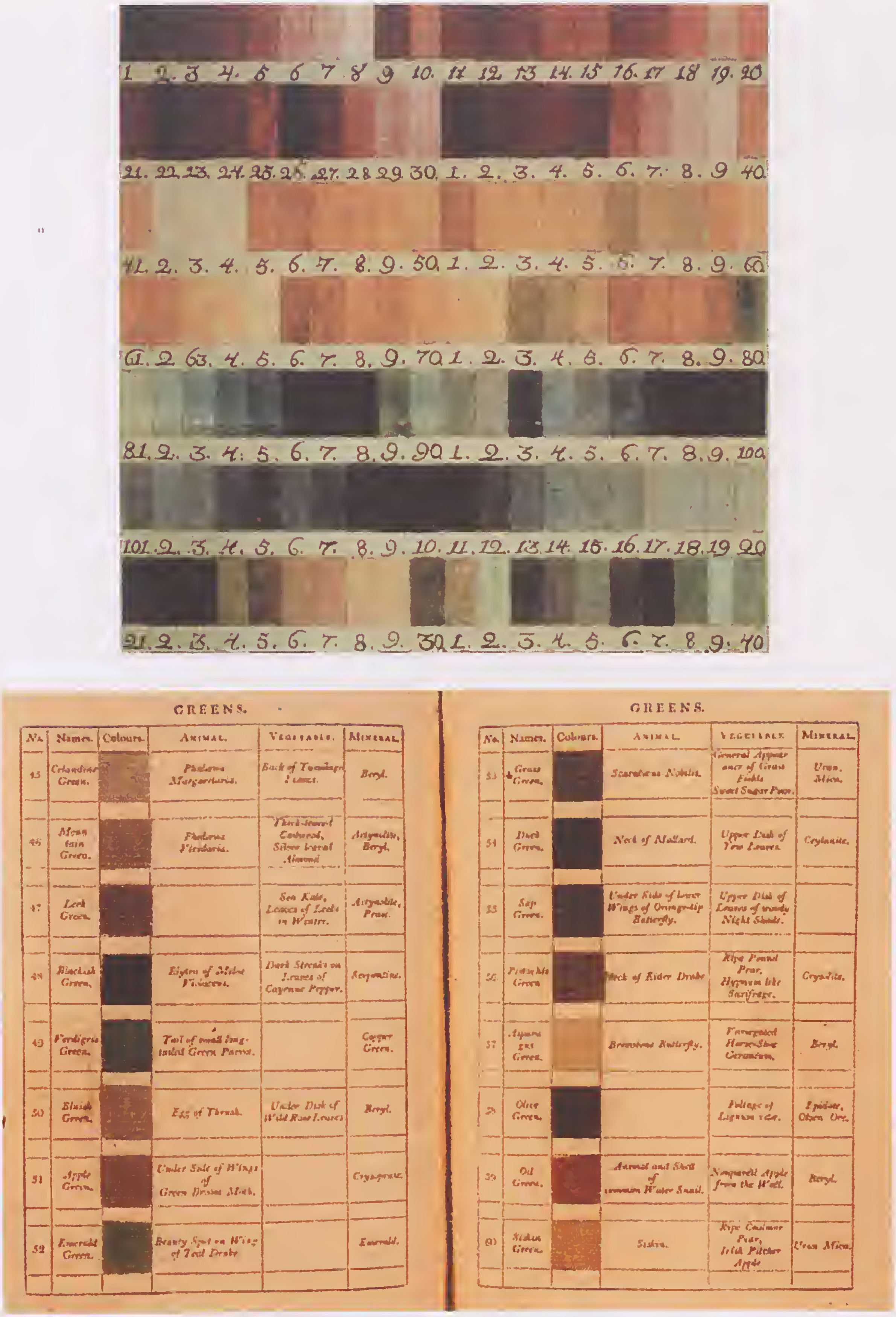
[3] Notes: There are several blackbutts not included, all have black feet of trunk. Some indigenous names are simply spelling/alliteration changes but are added to give perhaps greater insight into their pronunciation. "*The bark of many eucalypts is smooth and shed annually, and the new and old bark can make a colourful contrast while this is happening. Other groups of eucalypts have persistent bark of varying texture, examples being the stringybark and ironbark groups*" (Cheifetz *et al* 1999).

a clear attempt to describe colour as keenly as possible, such as the "pale brownish-green" of new leaves of *Banksia attenuata* (George 1984a). However, neither discolorous nor concolorous give a colour within green. 'Green' produces particular problems of colour terminology, and gives rise to adjectives which are not colour descriptors, such as dull, deep, and shiny. Likewise, 'grey' produces further descriptors of light, silver, pale, and grey-white, grey-brown, grey-green, and simply grey. Examples of colours which refer to something else are "elephant grey" for *Banksia littoralis* (Seddon 1972) and "sap green" for new bracts of *B. menziesii* given by the artist Nikulinsky (1992). While it could be asked what species and which elephant, 'sap green' is a pencil-box colour in, for example, Derwent Artists (number 4900) and Faber-Castell (number 9201-167), where it is a standardised combination of colour pigment, minerals, wax, and agglutinant. 'Elephant green' and 'sap green' treat colour description in the same manner of Syme (1814) who refers, for example, to "Duck Green" as found in the "Neck of Mallard" (Figure 2B).

Discussion

What do these historical descriptions and lists reveal of colour description today?

Since William Dampier in 1688 noted Colour and two hundred years since the first scientifically-focussed explorers annotated colour in plant species in south-western Australia, descriptions of colour remain poor and variable. They are largely confined to base colours with no level of clarification. Leaves are green, dark, or light green, blue-green, glabrous, or pale. Yet is the green of one species the same as the green in another? In the Linnaean system plant classification is based primarily on sexual parts. Botanists since Linnaeus have sought physical features of high reliability and avoided superficial features in their descriptions. External features like the colours of bark and leaves are subject to variations due to seasonal changes, predation, ontogeny, time of exposure, life cycle of the plant, the nature of the season, varying water budgets, intra-species differences, and the age of the plant, and are thus avoided for


1 2. 3 4. 5 6 7 8 9 10. 11 12 13 14. 15 16. 17 18 19. 20
21. 22. 23. 24. 25. 26. 27. 28 29. 30. 1. 2. 3. 4. 5. 6. 7. 8. 9 40.
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81. 2. 3. 4. 5. 6. 7. 8. 9. 90. 1. 2. 3. 4. 5. 6. 7. 8. 9. 100
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21. 2. 3. 4. 5. 6. 7. 8. 9. 30. 1. 2. 3. 4. 5. 6. 7. 8. 9. 40

GREENS.

No.	Names.	Colours.	Animal.	Vegetable.	Mineral.
45	*Celandine Green.*	■	*Phalaena Margaritaria.*	*Back of Tussilago Leaves.*	*Beryl.*
46	*Mountain Green.*	■	*Phalaena Viridaria.*	*Thick-leaved Cudweed, Silver-leaved Almond*	*Actynolite, Beryl.*
47	*Leek Green.*	■		*Sea Kale, Leaves of Leeks in Winter.*	*Actynolite, Prase.*
48	*Blackish Green.*	■	*Elytra of Meloe Violaceus.*	*Dark Streaks on Leaves of Cayenne Pepper.*	*Serpentine.*
49	*Verdigris Green.*	■	*Tail of small long-tailed Green Parrot.*		*Copper Green.*
50	*Bluish Green.*	■	*Egg of Thrush.*	*Under Disk of Wild Rose Leaves*	*Beryl.*
51	*Apple Green.*	■	*Under Side of Wings of Green Broom Moth.*		*Crysoprase.*
52	*Emerald Green.*	■	*Beauty Spot on Wing of Teal Drake*		*Emerald.*

GREENS.

No.	Names.	Colours.	Animal.	Vegetable.	Mineral.
53	*Grass Green.*	■	*Scarabaeus Nobilis.*	*General Appearance of Grass Fields Sweet Sugar Pear.*	*Uran Mica.*
54	*Duck Green.*	■	*Neck of Mallard.*	*Upper Disk of Yew Leaves.*	*Ceylanite.*
55	*Sap Green.*	■	*Under Side of lower Wings of Orange-tip Butterfly.*	*Upper Disk of Leaves of woody Night Shade.*	
56	*Pistachio Green*	■	*Neck of Eider Drake*	*Ripe Pound Pear, Hypnum like Saxifrage.*	*Crysolite.*
57	*Asparagus Green.*	■	*Brimstone Butterfly.*	*Variegated Horse-Shoe Geranium.*	*Beryl.*
58	*Olive Green.*	■		*Foliage of Lignum vitae.*	*Epidote, Olive Ore.*
59	*Oil Green.*	■	*Animal and Shell of common Water Snail.*	*Nonpareil Apple from the Wall.*	*Beryl.*
60	*Siskin Green.*	■	*Siskin.*	*Ripe Coalmar Pear, Irish Pitcher Apple*	*Uran Mica.*

Figure 2. An early colour grid of Ferdinand Bauer (Lack & Ibáñez 1997) (top) and part of the colour grid of Syme (1814) (bottom). Bauer's grid has 140 colours. Syme's grid has 108 hand-painted colour samples arranged in groups and including reference to the colour in nature in animal, vegetable and mineral. These colours are no longer true as they have faded with time and altered with reproduction.

Table 2

Examples of descriptions of leaf and bark colour in flora of south-western Australia in existing literature to indicate variation in colour description. Fuller descriptions are available from the author for *Acacia cyclops, A. rostelliferra, A. saligna, Agonis flexuosa, Allocasuarina fraseriana, Banksia attenuata, B. grandis, B. ilicifolia, B. littoralis, B. menziesii, B. prionotes, Callitris preisii, Casuarina obesa, Corymbia calophylla, Dryandra sessilis, Eucalyptus accedens, E. argyphea, E. caesia, E. decipiens, E. diversicolor, E. gomphocephala, E. marginata, E. rudis, E. todtiana, E. wandoo, Jacksonia furcellata, Kunzea ericifolia, Melaleuca cuticularis, M. huegelii, M. lanceolata, M. preissiana, M. rhaphiophylla, M. teretifolia, Nuytsia floribunda, Pittosporum phylliraeoides, Santalum acuminatum, Xanthorrhoea preissii.*

Species	Plant part	Description
Banksia attenuata R Br.	New leaf	Pale brownish-green (George 1984*a*)
	Mature leaf	Deep green and shining above, pale below (George 1984*a*)
Banksia grandis Willd.	Mature leaf	Shiny dark green above (Boland *et al* 1984); Deep-green (Seddon 1972); Dark green (George 1984a)
Banksia littoralis R.Br.	Mature leaf	Undersides are pure white (Powell 1990)
	Bark/trunk	Bark of trunk is elephant-grey (Seddon 1972)
Banksia menziesii R.Br	New bracts	Sap green (Nikulinsky 1992)
	Mature leaf	Dull green, pale below (George 1984a); Greyish-green (Powell 1990)
	Bark/trunk	Greyish-pink or pale brown (George 1984a)
Corymbia calophylla (Lindl.)K.D.Hill & L.A.S.Johnson	Mature leaf	Green, strongly discolorous (Boland *et al* 1984); Dark green, strongly discolorous (Chippendale 1988); Green to dark green above, pale below (Powell 1990); Strongly discolorous, dull, dark green above (Brooker & Kleinig 2001); Dark green above, distinctly pale green below (French 1997)
	Bark/trunk	Dusky-brown or reddish (Moore 1884, p.135); In young trees bark is grey but with age becomes brownish to dark grey, and is frequently stained in patches to a reddish hue by the kino which exudes from the tree (Boland *et al* 1984); Grey, but coarser and darker than the bark of tuart, and may be stained a rusty colour from exuded kino (Seddon 1972); Bark grey (Marchant *et al* 1987); Grey or grey-brown (Chippendale 1988); Bark grey, often exudes a reddish-brown gum from trunk or branches (Powell 1990); Grey to grey-brown (French 1997)
Eucalyptus accedens W. Fitzg.	New leaf	Greyish-blue to glaucous, concolorous to slightly discolorous; in intermediate stage dull, bluish green or grey-green, concolorous (Boland *et al* 1984); More or less glaucous (Marchant *et al* 1987); Grey-blue or glaucous, concolorous (Chippendale 1988)
	Mature leaf	Dull, bluish green or grey-green, concolorous (Boland *et al* 1984); Blue-green or grey green (Chippendale 1988)
Eucalyptus gomphocephala DC	New leaf	Green, discolorous; green concolorous at intermediate stage (Boland *et al* 1984); Blade light green (Marchant *et al* 1987); Green, discolorous (Chippendale 1988); Light green above, paler below (French 1997); Discolorous, light green (Brooker & Kleinig 2001)
	Mature leaf	Green, concolorous (Boland *et al* 1984); Light green, dull sheen (Holliday & Watton 1980); Grey-green (Marchant *et al* 1987); Greyish mid-green (Powell 1990); Grey-green (Rippey & Rowland 1995); Shiny green; slightly discolorous to concolorous even on same tree (French 1997); Slightly discolorous to concolorous, glossy, light green (Brooker & Kleinig 2001)
	Bark/trunk	Light grey (Boland *et al* 1984); Silver-grey (Seddon 1972); Grey-brown or grey (Holliday & Watton 1980); Grey (Rippey & Rowland 1995; Chippendale 1988; Powell 1990); Pale grey (Marchant *et al* 1987); Paler patches to pale grey (Powell 1990); Grey to grey-white bark (French 1997); Dark grey (Brooker & Kleinig 2001)
E. todtiana F.Muell.	Mature leaf	Paler green than the other eucalypts of the coastal plain (Seddon 1972); Dull green (Marchant *et al* 1987); Green (Chippendale 1988); Dull and pale (Powell 1990)
Melaleuca preissiana Schauer	Bark/trunk	Whitish to light brownish (Boland *et al* 1984); White papery bark (Seddon 1972); White chartaceous (Marchant *et al* 1987); Whitish, papery (Powell 1990)
Santalum acuminatum (R.Br.) A. DC	Mature leaf	Pale green-yellow (Powell 1990); Yellow-green (Rippey & Rowland 1995)

taxonomic purposes. For examples, salmon gum *Eucalyptus salmonophloia* appears more salmon as autumn approaches and the trunk of tuart, the white gum *E. gomphocephala*, appears almost black after heavy winter rains. Botanists have thus restricted their descriptions to those features which are not affected by the environment, such as leaf venation, and oil gland patterns, and flower bud characters before operculum shed, such as stamen inflexion and ovule rows. These features are regarded as immutable. And yet, curiously for science since the Enlightenment, this has resulted in an absence of complete description, and a form of colour blindness. Those who simply recorded what they saw, such as Dampier, botanical illustrators such as Bauer, and settlers such as Mrs Millet, saw more detail in colour than modern texts usually suggest.

Authors are clearly struggling to describe leaf colour. What colour is dull green? What colour is dark green? Deep green? Grey green? Mid green? Green is given in the historic and existing literature as dark, light, mid, and pale, but with few indications as to whether the hue is of yellow, grey, or blue, with no indication possible of how yellow, grey, or blue. An exception is, for example, the note that blue-leaved jarrah *E. marginata* subsp. *thalassica* has bluish leaves. This is a very different colour to that of tallerack, *E. pleurocarpa*, or mottlecah *E. macrocarpa*, both denoted in the modern literature as glaucous. Glaucous itself is a unique and somewhat confusing expression in botany, for although it comes from the Greek *glaukos*– bluish-green, silvery, or grey – its usually means that the surface is covered with a white wax which can be rubbed off. When colour-coded with the Natural Color System of Sweden (NCS), glaucous surfaces fall very clearly in the 'bluish' range (Grose, unpublished) and thus the term remains in this study as an indicator of leaf colour seen by an observer.

Even when leaves are the most telling difference visually to the species, leaf colour is not well described in the either old or modern literature. For example, *E. plurocaulis* is purple-leaved, but it is difficult to define purple, and when blue becomes purple, or when red becomes purple. This difficulty is shown in the comments by Pignatti-Wikus *et al* (2000a), regarding the colour-code of Bauer, that the colour for flower parts given by Bauer's code and that of modern botanical description varies from red to purple. Likewise, the leaves of *Santalum acuminatum* are described as both "green-yellow" and "yellow-green" (Table 2) suggesting in the first an emphasis on yellow and in the latter an emphasis on green, a major distinction in colour systems such as the NCS.

Descriptions in the literature do give indications that several colours might exist in leaves, with the distinction of concolorous (all of one colour) and discolorous (more than one colour). The physiological basis of discolorous and concolorous derives from the nature of the internal arrangement of the photosynthetic tissue within the leaf, with concolorous being those with isobilateral arrangements, but the situation is not always clear-cut (Brooker, *pers. comm.*). While indicating multiple colours, the term discolorous does not inform the reader of what colours might be present. Less clear is the reference to "*slightly discolorous*", as given for *Eucalyptus gomphocephala* (Table 2).

Even when considering adaxial (upper) and abaxial (lower) leaf surfaces, which are often a source of colour differentiation, the description can be 'green above, paler below', such as for *Banksia attenuata* and *Corymbia calophylla* (Table 2). Since the abaxial surface is specialized for gas exchange and is considered as old as land plants themselves and derived from the stem, and the adaxial an innovation in leaf evolution (Cronk 2001), it is enticing to speculate on how the adaxial leaf grew 'darker above' in response to the capture of solar energy during the Palaeozoic.

Trunk descriptions of brown give no indication as to whether the brown is red, yellow-based, or has much black or white, and if white, what white? Even for species noted for an unusual trunk colour, the colour is often not well described. For example, Baudin described *Xanthorrhoea preissii* as having a "*coal-coloured trunk*" (Baudin 31 May 1801) but this feature is not mentioned in more modern texts. Even where there has been an accompanying photograph, which might have excused the lack of colour description, it has not been clear whether the plant was in deep shadow, or coal black. Mrs Millet (1872) noted that the colour of *X. preissii* "*...is not naturally black, but brown; nevertheless, most of them are so completely blackened by bush-fires...*", facts supported by the leading *Xanthorrhea* salvage specialist in Western Australia (*Xanthorrhoea preissii* is salvaged from those areas which are under suburban development, and from road-widening areas). It is notable that some more recent descriptions of species do attempt to suggest that there is a range of colour within one trunk, particularly in the trees which shed their bark annually, such as the salmon gum *E. salmonophloia*.

While the expression 'green above, paler below', the title of this paper, tells someone keying out in the field what to look for, it does not allow someone else to compare the colour with a species elsewhere, or to know what the colour might be. Like Bauer, who was able to paint Australian trees from numbers with great confidence and accuracy while in London, a colour 'fingerprint' or 'portrait' would give both a clearer picture of which colours make up discolorous, which colour is found as concolorous, what colour is green, and what colour is 'paler below', and enable comparisons of colour in flora across the globe. However, Table 2 suggests that modern colour descriptions remain at a level which does not allow the scientific rigour of comparison or analysis of this important aspect of the flora.

Can we examine colour across places?

While current descriptions acknowledge colour variation to some degree, and are useful for casual observation and botanical description in the field, the level of colour description does not facilitate rigorous comparison between species. Colour hues and nuances are not detailed. Thus, even after two hundred years of collecting in Australia, the literature provides inadequate complexity in the description of the colours in Australian trees. While descriptions of colour remain embedded in botanical description within a classification system based on sexual parts, we remain unable to compare the colours of endemic species, genera, or families, and to determine the range of colour found within one continent, or to perhaps compare Laurasian floras with Gondwanan.

Colour has long been acknowledged as a difficult subject to study (Gage 1993). However, it has also been long recognised as an essential part of description, as exemplified by Syme's (1814) introduction to a discourse on the colour of plants in which he wrote: "*A nomenclature of colours, with proper coloured examples of the different tints, as a general standard to refer to in the description of any object, has been long wanted in arts and sciences. It is singular, that a thing so obviously useful, and in the description of objects of natural history and the arts, where colour is an object indispensably necessary, should have been so long overlooked. In* *describing an object, to specify its colours is always useful; but where colour forms a character, it becomes absolutely necessary. How defective, therefore must description be when the terms used are ambiguous; and where there is no regular standard to refer to. Description without figure is generally difficult to be comprehended; description and figure are in many instances still defective; but description, figure and colour combined form the most perfect representation, and are next to seeing the object itself. An object may be described of such a colour by one person, and perhaps mistaken by another for quite a different tint.......and often one name indiscriminately given to many colours."* This last has been particularly true of every colour associated with plants.

In this paper on colour description I have attempted to draw out simply the poor level of colour description in the current literature, examining the major and more commonly visible and known trees of one place – the South-western Australian Floristic Region - in a little detail. Descriptions of colour in the region remain relatively unchanged from the early pre-colonial literature, and this situation is likely to be typical of the global picture. As Syme suggested two hundred years ago - at the time of many of the early scientific expeditions to Australia and the use of colour grids for painting - figure, description, and colour combined would form the "most perfect" representation of a plant species. It is colour which has been neglected due to its difficulties. More detailed and precise colour description will enable comparisons to be made between the flora of south-western Australia and others, allow for further discussion on the changing colours of Australian environments with plant introductions, and give attention to colour as an aspect of global biological diversity.

Further, while botanists might learn to use the added external and changeable features of colour to botanical literature as a 'more perfect' representation, artists and those in the design professions might also benefit from specific, reproducible colours of flora to further understand the 'geography of colour' (Lenclos 1989). It is hoped that with more accurate description, more light will be shed on the immense beauty and biological diversity of this south-western Australian flora, and others.

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Shape and spatial distribution of Mulgara (*Dasycercus cristicauda*) burrows, with comments on their presence in a burnt habitat and a translocation protocol

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Abstract

The Crest-tailed Mulgara (*Dasycercus cristicauda*), a species listed as vulnerable under the Commonwealth Environment Protection and Biodiversity Conservation Act (1999) and as a Schedule 1 species under the Western Australian Conservation Act (1950), was once found throughout arid central Australia and Western Australia, but its geographic range has been significantly reduced. The spatial distribution and shape of Mulgara burrows is described for an area that was subsequently cleared in the Pilbara of Western Australia. The area contained a substantial cover (» 50% cover) of spinifex (*Triodia* sp.) tussocks to about 600 mm high and scattered shrubs when first searched in June 2006 but had been burnt (November 2006) by the time Mulgara were to be translocated before the vegetation was cleared in January 2007. Burrows contained between two and nine entrances, tunnels were mostly on a single level and to a depth of about 300 mm. The lumen for a burrow entrance was typically an arch over a flat bottom with a height of 70–80 mm, and a width of 80–100 mm at the base. Internal tunnels were mostly 50–70 mm wide. Burrows entrances in the burnt landscape were mostly in the open. There was one burrow per 2.5 ha in the area searched, but this was probably a 'hot-spot' for Mulgara for the region. Four Mulgara were caught in 750 Elliott trap-nights and five by digging out 65 recently active burrows in an area of about 22 ha. From this we concluded that a substantial trapping effort was required to trap all the Mulgara in an area. If Mulgara are being translocated from an area, then we would recommend an intensive trapping program combined with searching for and digging out all recently active burrows in the area. Strategies to enhance the capture of Mulgara are discussed.

Keywords: Mulgara, *Dasycercus cristicauda*, burrows, Pilbara, Western Australia

Introduction

Two species of Mulgara are currently recognised, the Crest-tailed Mulgara (*D. cristicauda*) and the Brush-tailed Mulgara (*D. blythi*: Woolley 2005). As this taxonomic change was recent, it is likely earlier reports on Mulgara referred to one or both species. This paper discusses the shape and spatial distribution of Crest-tailed Mulgara burrows.

Mulgara are generally sedentary in contrast with some other small dasyurids and have high site fidelity and a low propensity for dispersal once a home range has been established (Masters 1998, 2003; Dickman *et al.* 1995). Home ranges vary in size from 1.0 to 14.4 ha (mean 6.5 ha, Masters 2003), with some overlap.

Both males and females use 2–9 burrows, but average about three (Masters 2003). Burrows are mostly used by a single individual, but males and females have been found together in a single burrow during the breeding season (Masters 2003). An individual's burrows are likely to be concentrated in a relatively small area as the average maximum distance across a home range is about 440 m (Masters 2003). Woolley (1990) described *D. cristicauda* burrows near Ayers Rock as having one large hole, around which there was loose soil, and either one or two smaller holes within 1 m of the large hole. The tunnels to these pop holes were near vertical. Tunnels in these burrows led to a grass-lined nest at a depth of about 0.5 m. Each of these burrows contained a female with pouched young. Strahan (2000) suggested that the complexity of burrows varies geographically with those in central Australia having a single entrance with two or three side tunnels and pop holes, and those in Queensland having more than one entrance, deeper branching tunnels and numerous pop holes. This difference may have been due to differences in species that were not recognised until recently. It is therefore apparent there are limited data in the literature that describe the shape of Mulgara burrows and there is nothing on their spatial distribution.

Masters *et al.* (2003) reported that *D. cristicauda* can tolerate a moderate local reduction of vegetation cover, but suggested that a more severe reduction could result

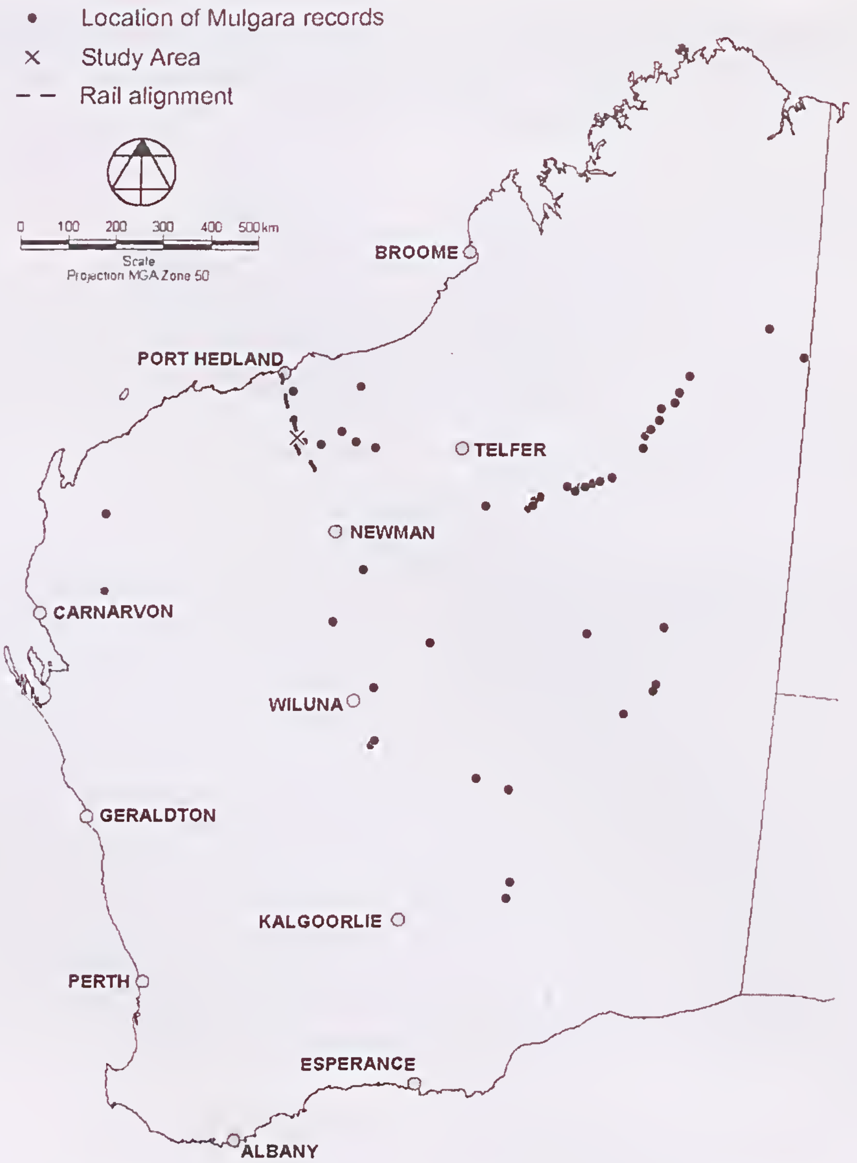

Figure 1. Capture locations of Mulgara in the Western Australian Museum collection, location of the Fortescue Metals Group railway line corridor and the location of the study site (marked with an X).

in a population decline (Masters 1993). In contrast, in this investigation we report on numerous active burrows in an area that had been burnt and was largely devoid of vegetation. Staff in Fortescue Metals Group indicated that the area was burnt during the early part of November 2006.

This case study focuses on a particular site that was to be cleared once Mulgara had been translocated. Fortescue Metals Group is constructing a railway line from Port Hedland to their Cloud Break mine about 260 km to the south (Figure 1). In order to meet its environmental obligations the proposed railway line corridor and the associated borrow pits were searched between June and October 2006 to identify areas that might contain species of conservation significance including *D. cristicauda*. Areas recorded as containing species of conservation significance [Mulgara are listed as vulnerable under the Commonwealth Environment Protection and Biodiversity Conservation Act (1999) and as a Schedule 1 species under the Western Australian Wildlife Conservation Act (1950)] were again searched in December 2006 and January 2007 with the purpose of relocating individuals before clearing commenced (Table 1).

This paper reports on the shape and spatial distribution of Mulgara burrows in an area to be cleared, their presence in a burnt habitat and a protocol for catching Mulgara when they need to be translocated out of an area that is to be cleared.

Table 1

Sequence of search and trapping activity.

Date	Activity
26 June 2006	Searched the area – 22 person hrs
November 2006	Area burnt
20 December 2006	Searched the area
5–10 January 2007	Site was trapped, searched and all recently active burrows dug out

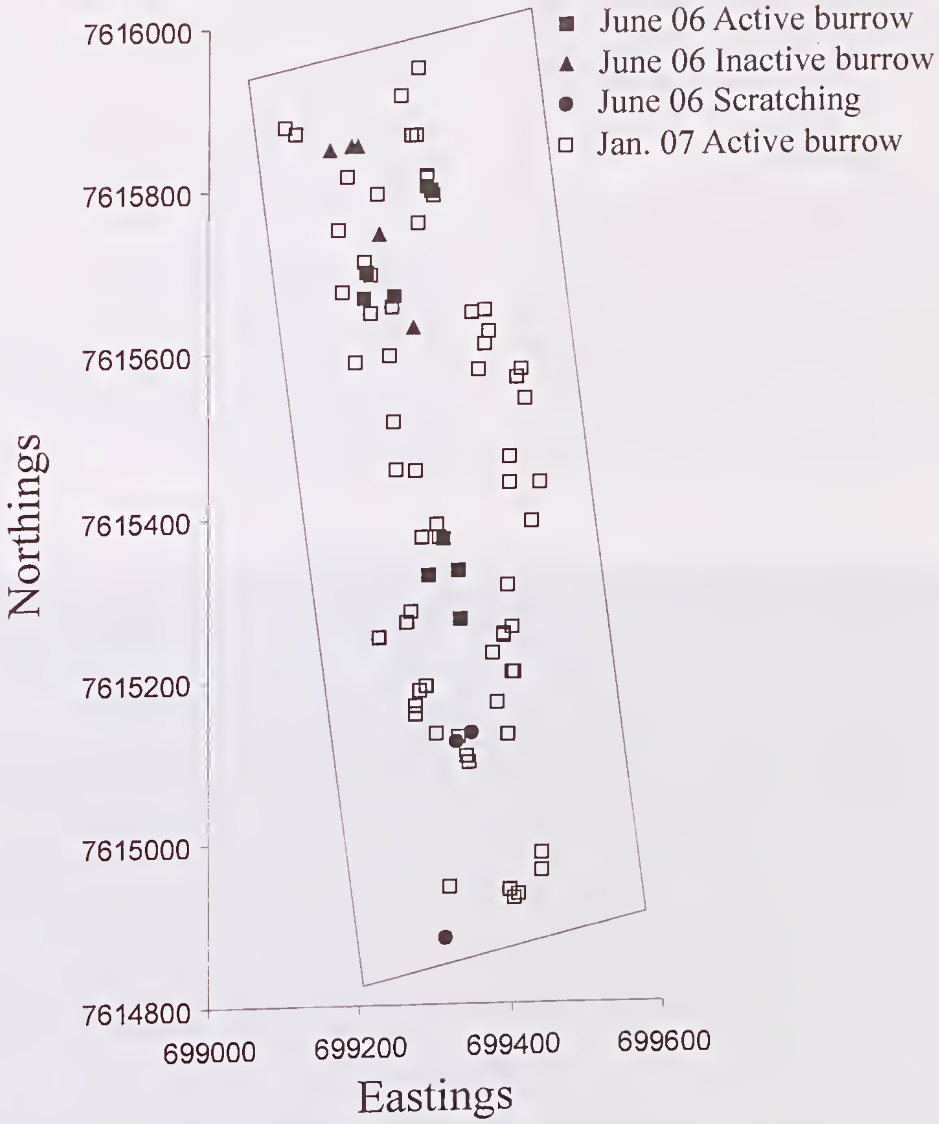

Figure 2. The parallelogram indicates the size and location of the area intensively searched and the location of burrows and scratchings detected in the June 2006 and dug out in January 2007.

Methods

Study site

The area intensively trapped and searched was a parallelogram of about 1100 m by 400 m on the Fortescue Metals Group railway line corridor (Datum WGS 84, UTM 50 699200E 7615700N; Figures 1 and 2). The site was vegetated with a substantial cover (» 50% cover) of spinifex (*Triodia* sp.) tussocks to about 60 cm high and scattered shrubs on a substrate of gritty red sand when first surveyed in June 2006 (Figure 3). It was to be cleared once the Mulgara in the area had been translocated.

Surveys

During June 2006, this site was systematically searched for Mulgara burrows, diggings and scats (Table 1). This involved five people walking in a line approximately 20 m apart up and down the site on four occasions (22 person hrs). The location of all active and inactive burrows, diggings and scats was recorded with a GPS. The area was well vegetated with spinifex and not all burrows would have been detected.

A pre-clearing survey was undertaken on 20 December 2006 to determine whether *D. cristicauda* burrows were still being actively used. Between 5–10 January 2007, 150 Elliott traps baited with peanut butter, rolled oats and sardines were deployed around the 22 ha site. These traps were left open for a period of five nights, a total of 750 trap nights. During that same period the entire area was systematically searched by up to four people on four occasions looking for recently active burrows. A recently active burrow was defined as one that had obvious signs of mammal movement around the entrance. Often there were multiple entrances to a burrow complex but only one entrance needed to show signs of recent activity for the burrow complex to be recorded as being active. All recently active burrows were excavated between 7 and 10 January 2007, initially by shovel to remove the surface soil and then by hand.

The dimensions of three burrows that contained

Mulgara were measured and have subsequently been drawn as figures. The location of all recently active burrows recorded during January 2007 was recorded with a GPS.

Results

In November 2006 the area was extensively burnt presumably from lightning strikes leaving a few isolated clumps of spinifex in a flat barren landscape that contained the occasional burnt trunk of shrubs and small trees. Figure 3 includes an image of the site that was taken in June 2006 and in January 2007. By January 2007 many of the small trees had begun to sprout leaves. During the June 2006 pre-burn search nine recently active burrows, five inactive burrows and three Mulgara scratchings were recorded (Figure 2). When the area had been burnt and recently active burrows were more easily identified, 65 were located.

Four Mulgara were caught in Elliott traps and five were dug from their burrows. Two of the Mulgara were mature adults (male 91 g, female 70 g); the other six weighed were three males with a body mass of 49, 39 and 52 g and three females with a body mass of 37, 44 and 34 g; and one individual was not sexed or weighed.

The area searched and location of each of the recently active burrows recorded during the June 2006 and January 2007 surveys are shown in Figure 2. The plan and elevation of three burrows containing Mulgara are shown in Figures 4–6. Recently active excavated burrows had either no pile of soil or a flattened pile less than 20 mm high making them difficult to detect from a distance (Figure 3).

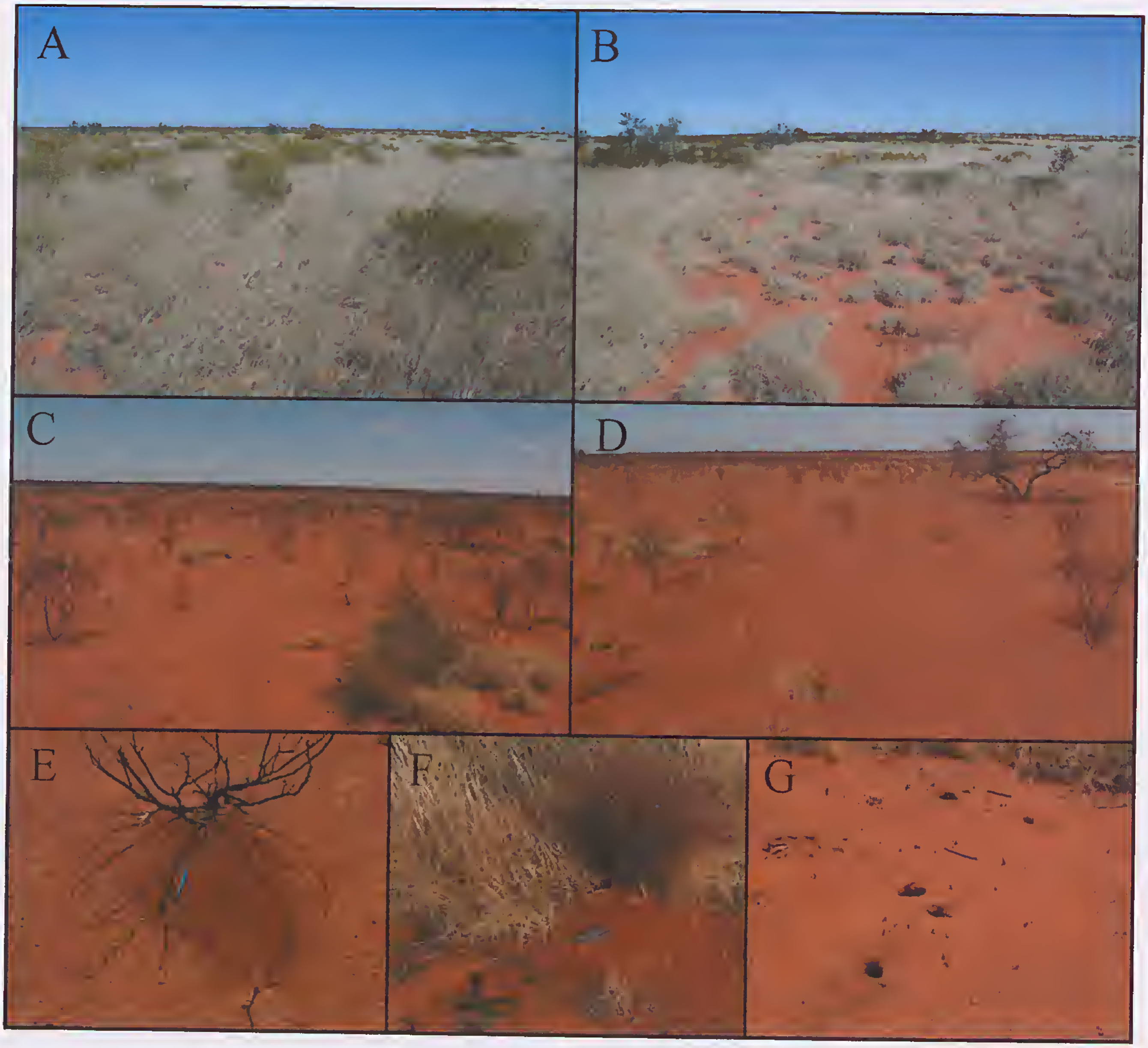

Figure 3. A and B show the habitat in June 2006 prior to burning; C and D show the habitat in January 2007 post burning; E, F and G show burrow entrances.

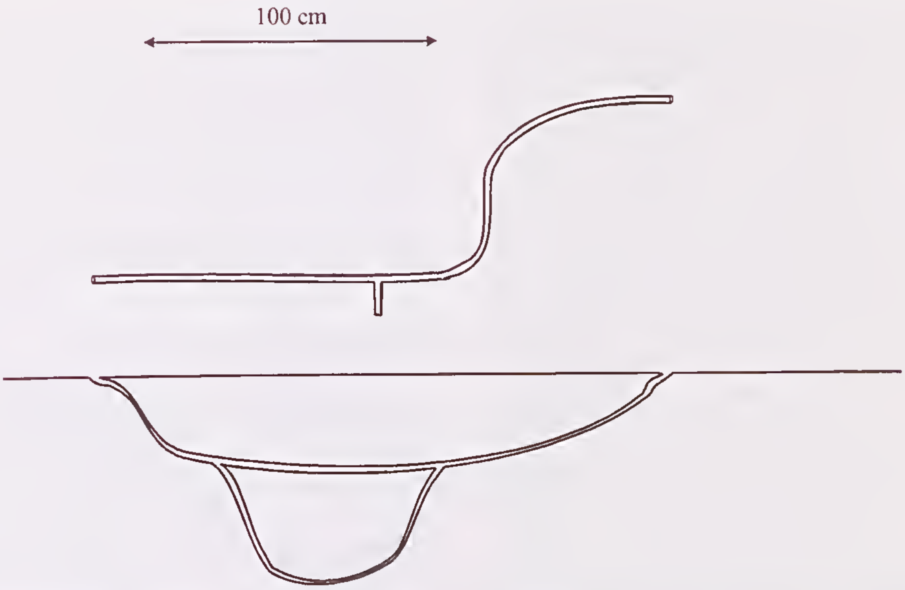

Figure 4. A plan and elevation of a burrow. The elevation is drawn as a casting with the surrounding soil being removed but a cross-section of the surface soil shown.

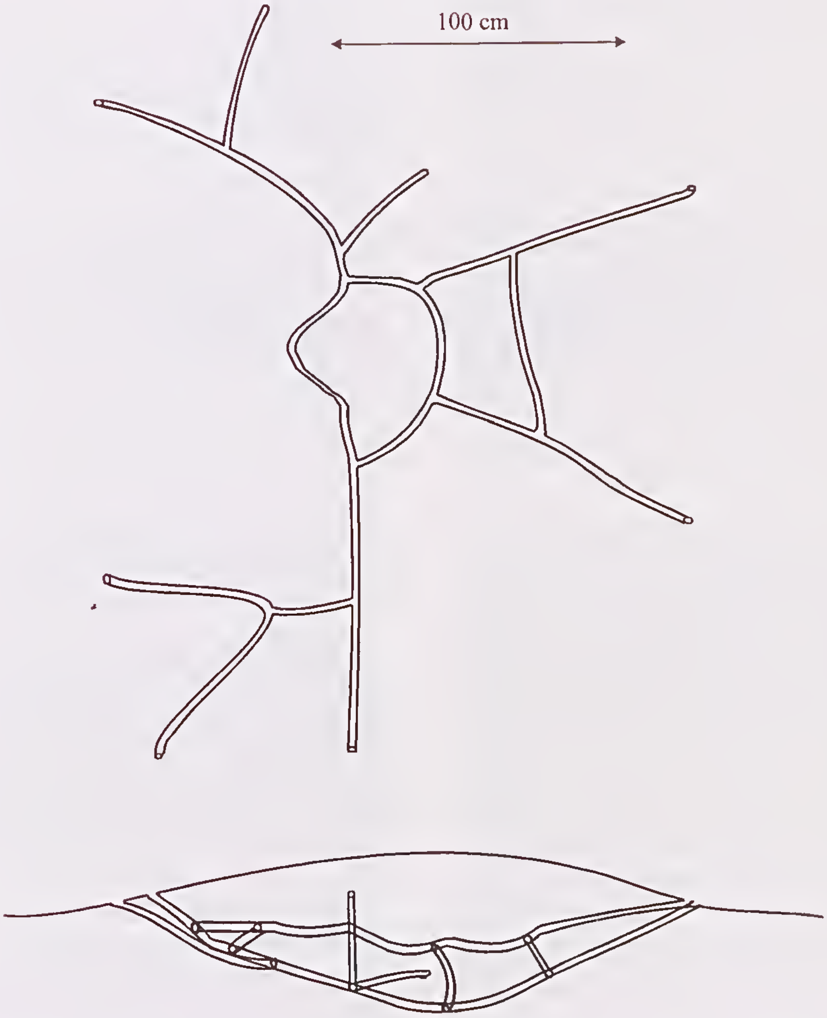

Figure 5. A plan and elevation of a burrow. The elevation is drawn as a casting with the surrounding soil being removed but a cross-section of the surface soil shown.

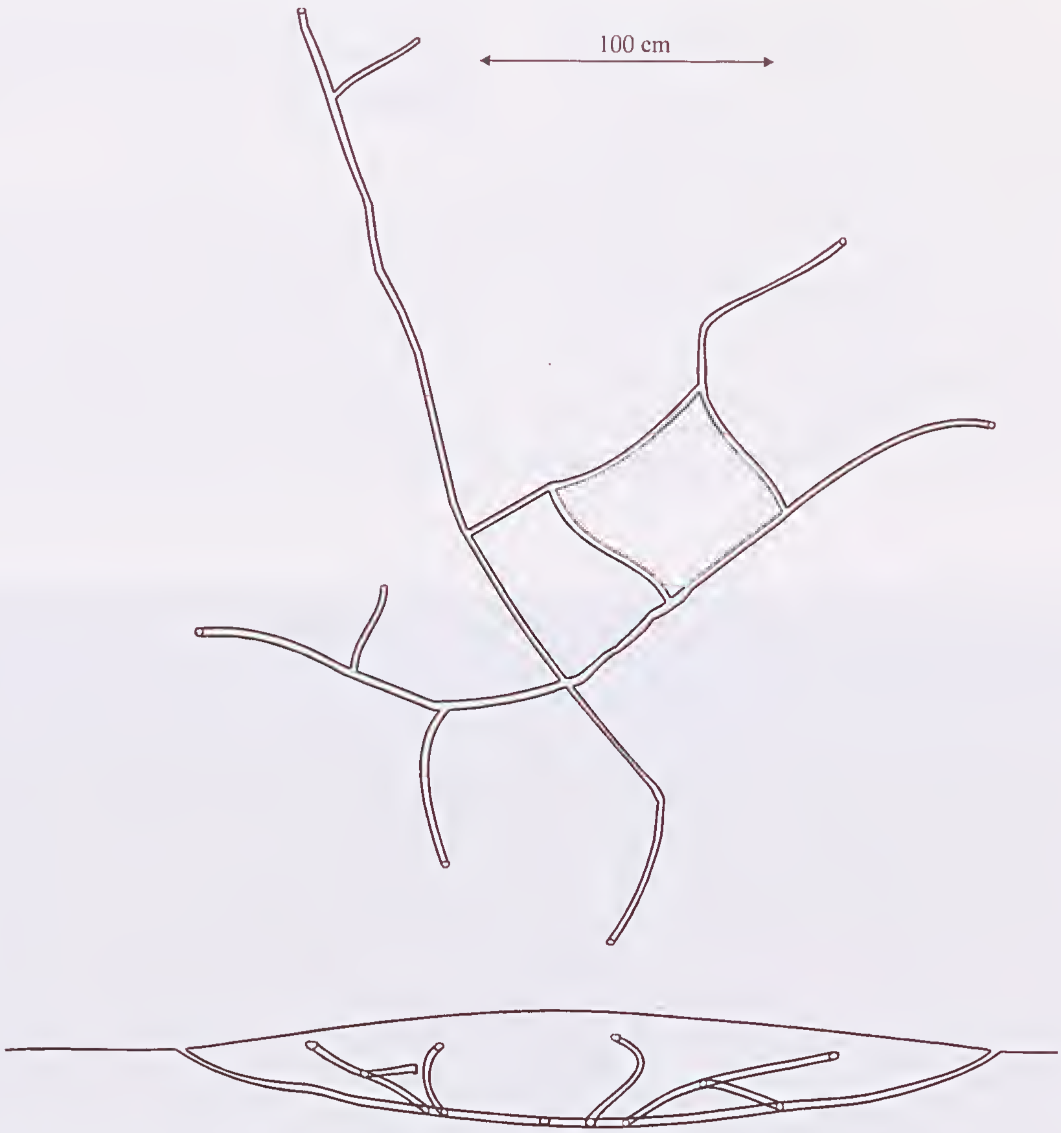

Figure 6. A plan and elevation of a burrow. The elevation is drawn as a casting with the surrounding soil being removed but a cross-section of the surface soil shown.

Based on the presence of a disturbed mound of soil at the burrow entrance, only two burrows had been recently dug out. Only six burrows were adjacent to a spinifex bush, all others were in the open (Figure 3, E, F and G). The complexity of burrows varied. Figures 5 and 6 show two of the more complex burrows. Some of the burrows were of a simple configuration with two entrances and a single joining tunnel or had one short blind tunnel leading off the main tunnel. Other burrow complexes had up to nine entrances. Burrows of a simple design and with few entrances mostly had a small mound of soil around the entrances (< 50 mm high), and some had no detectable mound of soil at all (Figure 3). None had a vertical shaft leading to a pop hole. Only two burrows contained tunnels that formed two levels, and one of these contained two Mulgara (Figure 4). The male was located in the blind spur off the tunnel closest to the surface and the female was in the deepest part of the lower tunnel. It should be noted that it takes up to an hour to excavate a burrow system and Mulgara probably move around the tunnels while the digging is going on so the capture location may not be where these individuals spent their day.

The lumen for a burrow entrance was typically an arch over a flat bottom with a height of 70–80 mm, and a width of 80–100 mm at the base. However, there was considerable variation with some entrances in a burrow complex looking very similar to that dug out by a *V. gouldii* which is much wider and not as high. Some burrow complexes contained entrances that were much smaller than these dimensions (*i.e.* 50–60 mm by 50–60 mm).

Internal tunnels were typically 50–70 mm wide. The deepest tunnel shown in Figure 3 was one of the narrowest excavated at 40 mm wide. Some burrow complexes contained enlarged sections, and these were mostly at the junction of tunnels. From the tracks around the burrow entrances, it appeared as if only a few of the entrances were in current use when there were up to nine entrances for some burrows. The deepest tunnel was generally less than 300 mm below the 'true' ground surface level, but mounds around burrow entrances meant that burrows could be up to 550 mm below the surface immediately above the deepest section of the burrow. Most burrows had only one level for all the tunnels. The burrow shown in Figure 4 is one of two burrows with two levels; the deepest section was approximately 650 mm below the surface and the other tunnel was about 250 mm below the surface at its deepest parts.

A *V. gouldii* (SVL » 200 mm) was found in one burrow complex with a Mulgara. This burrow was dug out at about 07:30 hr and the *V. gouldii* was very sluggish in its movements indicating that this was the burrow it had occupied the previous night. Two other burrows not containing Mulgara contained *Egernia striata*, one burrow contained five *Nephrurus levis*, one contained two *Pseudomys hermannsburgensis* and one contained a *Varanus eremius*. Elliott traps also caught two *Pseudomys hermannsburgensis* and one juvenile *V. gouldii* in addition to Mulgara.

Discussion

Masters *et al.* (2003) reported that harvesting (cutting the tops off all spinifex to a height of 15 cm) had no significant impact on the abundance of Mulgara in the arid desert around Ayers Rock, but Masters (1993) suggested a severe reduction in the vegetation could result in a population decline. Invertebrate biomass remained unchanged in the experimental plots of Masters *et al.* (2003); however, the mowing of the vegetation resulted in a significant reduction in the number of rodents caught in their study plots. In contrast with the findings of Masters (1993), our study site was burnt in November 2006, and it appears that Mulgara in the area did not move out of the burnt area. Immediately to the east of our study site there was an area which was not burnt and contained a dense cover of spinifex, and there was another area about 2 km to the north that was densely vegetated with mature spinifex on a sandy substrate. Both of these sites would seem to offer suitable alternative locations had the Mulgara wanted to move after the fire. These data suggested that Mulgara had adapted to the short term impacts associated with the removal of vegetation by fire.

There was no obvious clustering of recently active burrows within the area searched, however, it did appear as if there was a distinct linear orientation to the placement of burrows (Figure 2), as there were few burrows on the periphery of the area searched. A less intense search of the area outside the polygon (Figure 2) found no burrows. Some active burrows were located within metres of others (Figure 2) and there were some patches devoid of burrows. We could see no obvious reason for their specific locations; however, it may have reflected the presence of vegetation before the area was burnt.

The burning of the area made it much easier to locate burrows. As there was no evidence to indicate that new burrows had been dug (*e.g.* large piles of freshly disturbed soil at the burrow entrance) since the fire, we presumed that most of the burrows assessed as recently active went undetected in the June 2006 survey. Even when the area had been burnt the search effort to locate all recently active burrows was substantial (*i.e.* up to four persons on four separate occasions) indicating how difficult it was to locate some burrows.

Woolley (1990) and Triggs (2004) showed pictures of Mulgara burrows with substantial piles of soil around the entrance, but many of the burrows that we excavated burrows had either no pile of soil or a flattened pile less than 50 mm high making them difficult to detect from a distance. Those burrows with multiple entrances and associated mounds of soil to about 250 mm high were obviously easier to detect. Most of these were located adjacent to a clump of spinifex, some of which had been burnt. The pile of soil around the entrance provided no indication of the size, complexity or depth of the burrow that was underground. Given that the size of the mounds at the entrances to most burrows did not reflect the quantity of soil removed to dig the burrow, we concluded that most burrows had been there for a long time and the original mound of soil had been dispersed.

Woolley (1990) reported pop holes leading from a vertical shaft from Mulgara burrows; however, we found no burrows with this type of configuration. We have excavated many other burrows in the railway line corridor with vertical pop holes that were devoid of surrounding soil and never found a Mulgara but have occasionally found *Notomys alexis* (Thompson & Thompson 2007).

Our trapping effort (750 Elliott trap-nights) applied over an area of about 22 ha would normally be considered reasonably intensive, given the size of Mulgara's activity area. However, only four of the nine Mulgara captured were caught in traps. This has significant implications for other Mulgara trapping programs as they do not seem to be readily caught in baited Elliott traps. This study was part of a conservation significant fauna assessment and translocation program and had we relied solely on traps to capture all of the Mulgara in the area, then we would have either missed some and they would have died during the clearing process or, alternatively, the trapping program should have lasted for an extended period. These data demonstrate that digging out recently active burrows will reduce the time required to capture all of the Mulgara in an area. Further, digging out burrows in conjunction with trapping is likely to ensure that a greater proportion of the animals in the area are captured than if only traps were used. As the burning of the spinifex made it appreciably easier to locate all of the active burrows, we would recommend that a similar strategy be considered at other sites before a trapping and digging out of burrows program is undertaken to translocate Mulgara out of an area. We appreciate that this may not be possible for other sites, and we would urge that other impacts associated with burning the vegetation should be considered. However, when the area is to be cleared (by bulldozer) of vegetation immediately after all the Mulgara had been relocated any impacts that the fire might have had on the vegetation or other fauna will have been nullified.

As we only searched immediately outside of the area to be cleared and not more widely, we are unsure about the abundance of recently active burrows in the adjacent area, but in the area searched, the density of Mulgara was about one per 2.5 ha and the ratio of Mulgara to recently active burrows was about 1:7. Some of the burrows recorded as active by the marks around the entrance contained reptiles, so we may have over estimated the number of active Mulgara burrows. However, this number is low, with a maximum of five of the sixty five burrows in this category. This would reduce the ratio to 1:6.6. Most of the other areas searched in June 2006 along the railway corridor near the study site did not record high numbers of recently active and inactive burrows, so we concluded that this was a 'hot-spot' for Mulgara and this was the reason for the concerted effort to translocate individuals from this area before it was cleared.

It was apparent that if there were only nine Mulgara in the area and we located 60–65 recently active burrows, then *D. cristicauda* were utilising multiple burrows, probably each evening, which concurs with the findings of Masters (2003). Masters (2003) reported that it was rare to find two adults in the same burrow unless it was the breeding season. The largest two Mulgara that we caught were in the same burrow and the others were all caught by themselves.

Most burrow entrances were similar in size and shape suggesting that they had been initially dug out by Mulgara, but there were a few where the entrance looked very similar to the entrance of a *V. gouldii* burrow, suggesting that it was either initially dug out by a sand goanna or at some stage had been modified by a *V. gouldii*. The internal dimensions of the burrow tunnels were mostly uniform, with larger areas (perhaps nest sites) occurring at the junction of tunnels. The narrowest tunnel was about 40 mm wide, but most were 60–70 mm wide.

Although the horizontal layout of Mulgara burrows varied appreciably (see Figures 4–6), burrows were mostly of a uniform depth between 150 and 300 mm below the true ground surface level, but deeper if measured from the top of the mound of soil around the burrow entrances. This is a little less than the 400 mm reported for the burrow that Masters (2003) excavated in the Tanami Desert. For most burrows there was a single level, with only two burrows having tunnels on two levels. Mounds associated with burrow entrances near clumps of spinifex were often higher than those out in the open, which suggested that once the vegetation was removed, erosive forces were spreading the diggings from burrows over a larger area. Neither the orientation, location of burrow entrances nor tunnel configuration appeared to form a pattern, but the shafts down from the entrance for all burrows were gently sloping.

Acknowledgements: This project was undertaken during a pre-clearing fauna assessment for the Fortescue Metals Group railway corridor. The assistance and support of Fortescue Metals Group was most appreciated. Duanne Ginger, Greg Barrett, Luke Sibon and Rebecca Lee-Richie of Fortescue Metals Group/Team 45 and George Shredrawi assisted in searching the area and digging out burrows and their contribution was appreciated. Mulgara were caught under a licence issued by the Department of Environment and Conservation.

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Distribution, diet and potential ecological impacts of the introduced Mozambique mouthbrooder *Oreochromis mossambicus* Peters (Pisces: Cichlidae) in Western Australia

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Abstract

Oreochromis mossambicus is a highly successful invader of aquatic ecosystems due to its adaptable life history, trophic flexibility, ability to tolerate extreme and often unfavourable environmental conditions and maternal care of offspring. Upon introduction to areas outside of its natural range, these characteristics often give *O. mossambicus* a competitive advantage over indigenous fishes. Accordingly, *O. mossambicus* may have deleterious impacts on aquatic communities. Since nonindigenous *O. mossambicus* populations were first observed in Western Australia in the Gascoyne/Lyons River system (*ca* 25°S) in 1981, the species has spread north to the Lyndon and Minilya Rivers (*ca* 23°S), and south to the Chapman River (*ca* 28°S). There is a high probability of further range expansions of this cichlid in Western Australia due to natural dispersal and human-mediated translocation. Adult and juvenile *O. mossambicus* consumed primarily detritus and vegetal matter, though juveniles collected from the Gascoyne River were carnivorous. There was no demonstrable dietary overlap between *O. mossambicus* and the carnivorous and omnivorous sympatric species in the Chapman and Gascoyne Rivers. However, a statistically significant dietary overlap was noted between *O. mossambicus* and the native species *Craterocephalus cuneiceps* and *Hypseleotris aurea* in the Lyons River. Anecdotal observations of agonistic behaviour by breeding male *O. mossambicus* indicated that such behaviour was mainly directed towards other breeding males. The semi-arid climate of the Indian Ocean (Pilbara) Drainage Division results in the reduction of riverine habitats to small isolated pools during extended dry periods. Thus, in these restricted environments resource competition may occur between *O. mossambicus* and indigenous species.

Keywords: *Oreochromis mossambicus*, agonistic behaviour; cichlid; dietary overlap; freshwater fish; introduced species; tilapia; translocation

Introduction

The Mozambique mouthbrooder or tilapia, *Oreochromis mossambicus* (Fig. 1), is one of the most translocated freshwater teleosts worldwide (Arthington 1986; Blühdorn & Arthington 1990; Costa-Pierce 2003; Canonico *et al.* 2005). *Oreochromis mossambicus* is indigenous to fresh and brackish waters of southeastern Africa (Trewavas 1983; Skelton 2001) and has been cultured in many countries, most notably in Africa and Asia, for human consumption (Cadwaller *et al.* 1980). Their introduction into Australia was, however, as an ornamental species (Arthington 1986; Allen *et al.* 2002). Introduced *O. mossambicus* populations occur in tropical and subtropical areas of Australia including northeastern Australia (Queensland) and Western Australia (Arthington & Blühdorn 1994; Morgan *et al.* 2004). While the distribution and biology of the species has been well documented in Queensland (e.g. Arthington 1986; Arthington & Milton 1986; Blühdorn & Arthington 1990; Mather & Arthington 1991; Arthington & Blühdorn 1994; Blühdorn & Arthington 1994; Mackenzie *et al.* 2001; Russell *et al.* 2003; Canonico *et al.* 2005), little is known of its biology and potential impacts in Western Australia. This is of particular concern as the arid rivers in the Indian Ocean Drainage Division of Western Australia support five endemic freshwater teleosts with restricted distributions within this region (Morgan & Gill 2004).

Unfortunately, the characteristics that make *O. mossambicus* desirable as an aquaculture species also predispose it for success as an invasive species (Canonico *et al.* 2005). For example, the species is euryhaline and may reproduce in salinities from fresh to seawater (Laundau 1992; Skelton 2001), tolerates high concentrations of ammonia and nitrite (Popma & Masser 1999), tolerates wide temperature regimes and low

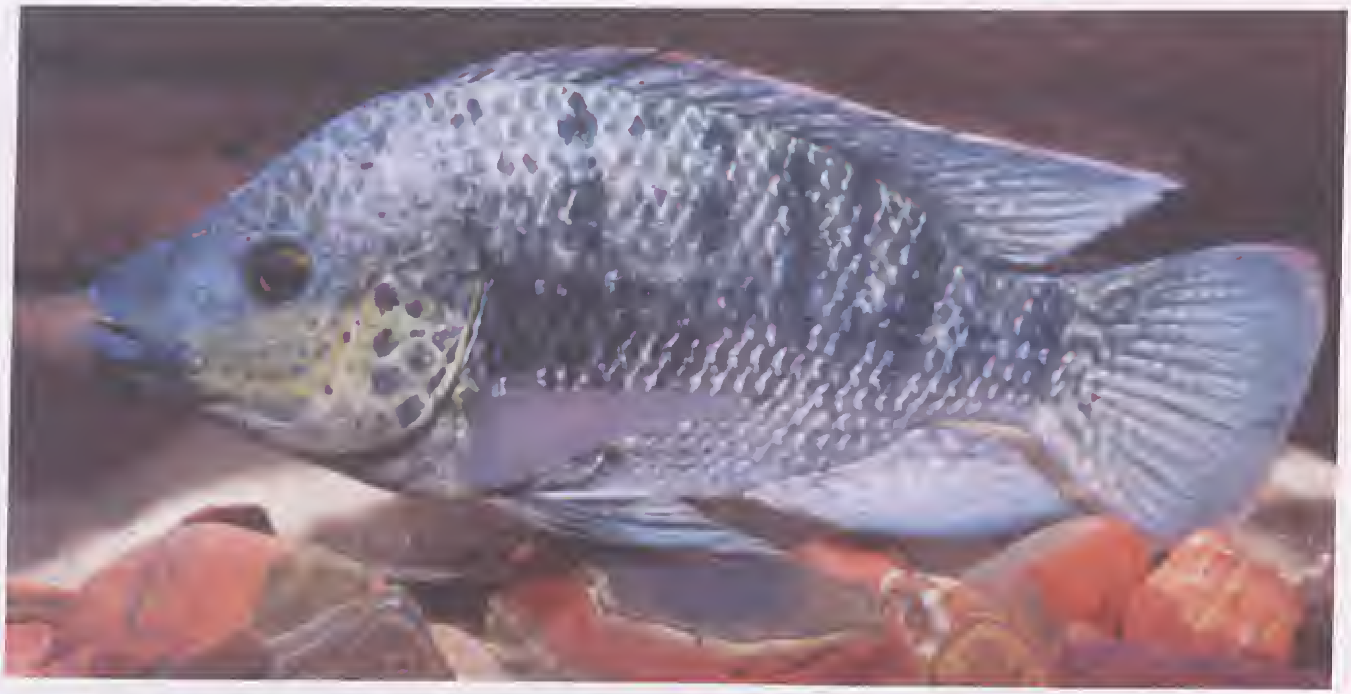

Figure 1. Male *Oreochromis mossambicus* collected from the Gascoyne River in Western Australia (198 mm standard length). (Photo: Mark Allen).

dissolved oxygen levels (Lovell 1998; Mackenzie *et al.* 2001), and is omnivorous, commonly consuming macrophytes, filamentous algae, phytoplankton, detritus and benthic organisms (Bruton & Boltt 1975; De Silva *et al.* 1984; Merrick & Schmida 1984; Arthington 1986; Laundau 1992). Furthermore, mouthbrooding (*i.e.* the maternal care of the fertilised eggs and newly hatched offspring) and protracted reproductive periods reduce the risk of offspring predation (Merrick & Schmida 1984).

There is a paucity of research on the precise environmental impacts of *O. mossambicus*, or the extent of competition, if any, between this introduced species and sympatric native fish in Australian waters and worldwide (Arthington 1986; Arthington & Blühdorn 1994; Mackenzie *et al.* 2001; Russell *et al.* 2003; Canonico *et al.* 2005). The high reproductive effort, growth rate, maternal care of offspring, and trophic and physiological flexibility enable the rapid establishment of *O. mossambicus*, often to the detriment of native species (Cadwaller *et al.* 1980; Canonico *et al.* 2005). *Oreochromis mossambicus* will also consume macrophytes (Arthington *et al.* 1994), which has led to their deliberate introduction, particularly in America, as a biocontrol agent (McCann *et al.* 1996, Helfman *et al.* 1997). This may lead to the disappearance of native aquatic plants when the species reaches high densities (Fuller *et al.* 1999). In Australia, *O. mossambicus* is a declared noxious species in Queensland and its importation into this country has been prohibited since 1963 (Arthington 1986; Blühdorn & Arthington 1990).

The occurrence of *O. mossambicus* in the Pilbara region provides the opportunity to examine the distribution, biology and potential ecological impacts of *O. mossambicus* in Western Australia, which are currently unknown. The persistence of the species in these often arid and unpredictable environments is most likely influenced by the ability to occupy unexploited niches, or to displace less competitive or smaller species. The successful colonisation of rivers (such as the Gascoyne River), which are exposed to irregular rainfall events and may remain as a series of small, disconnected pools for extended periods, may be to the detriment of native sympatric species. Thus, the objectives of this study were to document distribution and potential range expansions, provide baseline dietary data and discuss possible impacts of *O. mossambicus* in Western Australia.

Methods

Distribution and study sites

During part of a larger study by the Murdoch University Centre for Fish and Fisheries Research, sampling was undertaken in all rivers in the Indian Ocean (Pilbara) Drainage Division of Western Australia between December 2000 and November 2002 (see Morgan *et al.* 2003; Morgan & Gill 2004; Morgan *et al.* 2004). *Oreochromis mossambicus* was collected from the Chapman, Gascoyne, Lyons, Lyndon and Minilya rivers (Fig. 2). The Chapman River, at *ca* 28°S, is the most southerly location where this species occurs in Western Australia. *Oreochromis mossambicus* has been present in the Gascoyne River since 1981 (Allan *et al.* 2002), and rapidly spread throughout the main tributary, the Lyons River (Blühdorn & Arthington 1990). The Minilya and Lyndon rivers, just north of the Gascoyne River, represent the most recent range expansion of the species in Western Australia.

Sampling regime

Oreochromis mossambicus and sympatric species

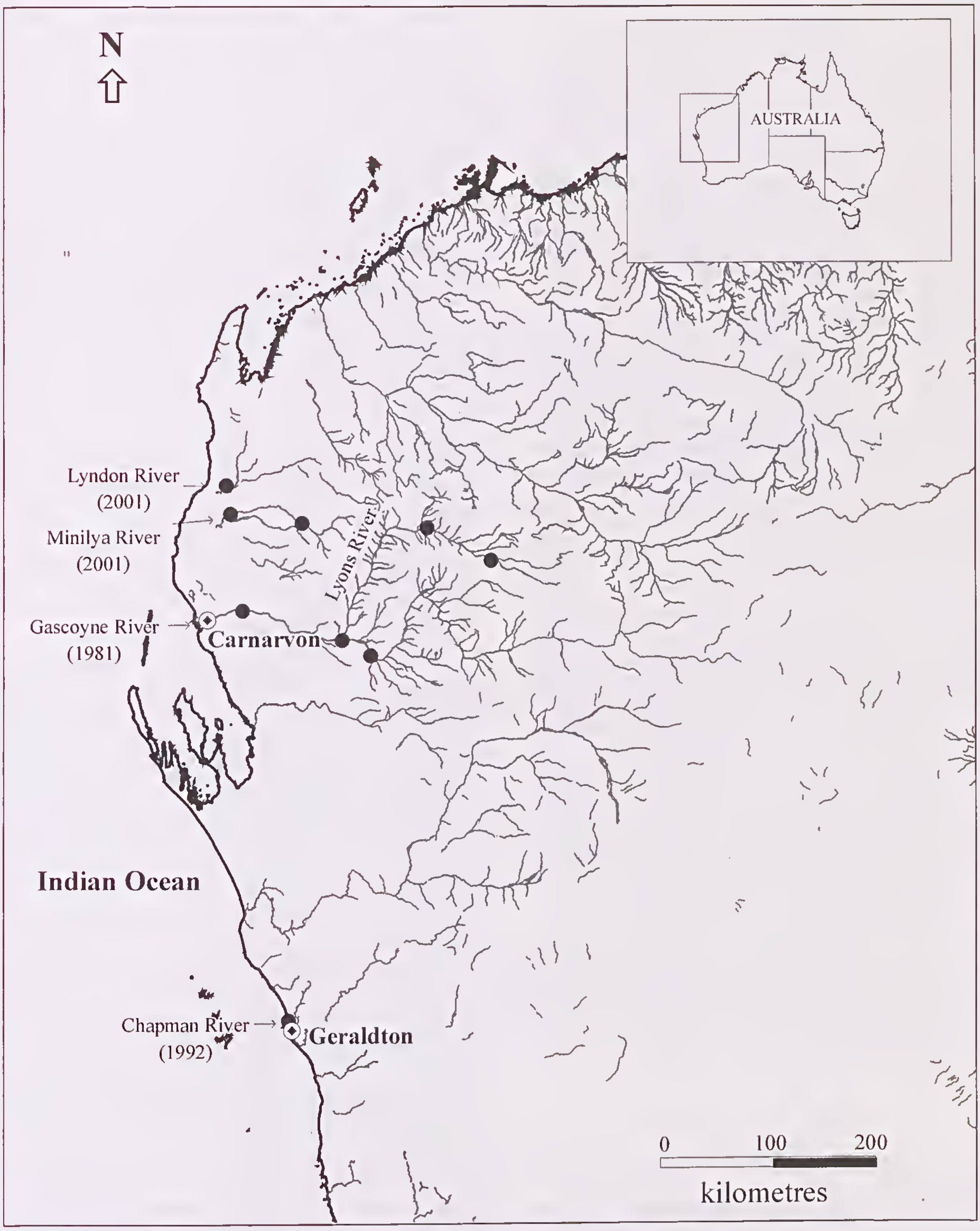

Figure 2. Sample sites (●) where *Oreochromis mossambicus* was collected in the Indian Ocean (Pilbara) Drainage Division of Western Australia. The year *O. mossambicus* was discovered in each river is included in parenthesis.

(where present) were collected with a seine net (either 21, 10 or 5 m seine net, with 3 mm mesh and 1.5 m drop). Seine samples were collected along banks adjacent to littoral and emergent vegetation (Chapman River, Lyons River), and across small pools (Gascoyne River). A small number of male *O. mossambicus* were collected utilising fishing lures in the Gascoyne River. A sub-sample of co-occurring species was retained for dietary analyses. After collection, specimens were anaesthetised and placed in 70% ethanol. Temperature, pH and conductivity were recorded from just below the water surface at each site when sampling.

Dietary analysis

The standard length (SL) of each fish was measured to the nearest 1 mm and the stomach, or in species that do not possess a well-defined stomach, the wide anterior section of the intestine was removed and inspected initially under a dissecting microscope. As *O. mossambicus* and other species collected were often detritivorous, the intestinal contents were inspected under a compound microscope (100–400 x magnification) and the small particulate matter identified to the lowest possible taxon. The diets of each species were analysed using the percentage frequency of occurrence and the percentage volumetric contribution of each dietary taxon (Hynes 1950; Hyslop 1980). The percentage frequency of occurrence is the percentage of all fish in a sample that have ingested a particular dietary item. The percentage volumetric contribution is the contribution of each taxon to the total gut contents of each fish, and was determined using the points method and estimates of stomach fullness (Hynes 1950; Hyslop 1980).

Volumetric data allow the best estimation of the relative importance of each dietary item (Hyslop 1980), therefore the percentage volumetric data for each individual dietary sample analysed were used to create similarity matrices for each species based on the Bray-Curtis similarity measure in the PRIMER v5.0 statistical package (Clarke & Gorley 2001). A one-way analysis of similarity (ANOSIM) was performed on the Bray-Curtis similarity matrices to provide a measure of dietary overlap between species, and between *a priori* designated size groups within the same species. ANOSIM is a non-parametric test that uses a permutation procedure applied to a ranked similarity matrix, based on, in this case, a Bray-Curtis similarity matrix. The test statistic R is a measure of the discrimination between groups, with a value of 0 indicating no differences between groups, and a value of 1 indicating that each member within an *a priori* designated group is more similar to other members of the group than it is to members of any other group. The significance value of each pairwise comparison (one-way ANOSIM) is used to indicate dissimilarity, with percentages below 5% (*i.e.* $p < 0.05$) usually considered statistically significant. Where possible, a more conservative significance level of $p < 0.01$ or $p < 0.001$ was highlighted in the results obtained. To graphically display differences and similarities in diets of the Chapman River fish samples, the Bray-Curtis similarity matrix was then classified using hierarchical agglomerative cluster analysis with group-average linking (Clarke & Gorley 2001).

Results

Chapman River study site

Oreochromis mossambicus was collected in the Chapman River estuary (114.631°E, 28.728°S) (Fig. 2). A small weir prevents the species' ingress upstream, thus, *O. mossambicus* is presently restricted to the lower reaches of this system. *Paspalum distichum* dominated the riparian vegetation creating a sheltered habitat at the waters edge, a characteristic that also makes this species a major weed of drainage channels in parts of Australia (Sainty & Jacobs 1994). Dietary analysis was conducted on three seasonal samples (*i.e.* spring, summer, autumn) of *O. mossambicus* and sympatric native species collected at this location (Tables 1, 2). No large *O. mossambicus* (*i.e.* greater than 112 mm) were collected.

A total of 4940 fishes comprising seven species was captured from the Chapman River study site in spring (24/10/02), summer (05/02/03), autumn (13/04/03) and winter (9/07/03) samples (Table 1), including two introduced fishes, *i.e. O. mossambicus* and *Gambusia holbrooki* (Poeciliidae), and five estuarine fishes, *i.e. Mugil cephalus* (Mugilidae), *Acanthopagrus butcheri* (Sparidae), *Amniataba caudavittata* (Terapontidae), *Hypseleotris compressa* (Eleotridae), and *Pseudogobius olorum* (Gobiidae). The prevalence of *O. mossambicus* and sympatric species varied greatly over four seasonal samples (Table 1). In spring, *O. mossambicus* comprised 12.7 % of collected specimens, and occurred at a density of 0.34 m^{-2} in the Chapman River. It was the fourth most prevalent species after *G. holbrooki* and two native fishes. In summer, the mean density of *O. mossambicus* increased markedly to 3.23 m^{-2}, and it was the most prevalent species (48.4 % of fish collected). This pattern continued in autumn with the mean density of *O. mossambicus* increasing to 8.47 m^{-2}. This cichlid was still the most prevalent species and comprised 64.1 % of fish collected. In winter the density of *O. mossambicus* decreased to 1.1 m^{-2} (34.3 % contribution), and was the second most abundant species after the indigene *P. olorum*. Over the year, the only native species captured in appreciable quantities were *H. compressa*, *P. olorum* and *A. butcheri* (Table 1).

Twenty-three prey items were identified from the intestinal tracts of *O. mossambicus* and six co-occurring species collected from the Chapman River in spring (Table 2). The bulk of the diet of small *O. mossambicus* was algae (60.9 %), with vegetal matter (10.9 %) and silt/biofilm (12.0 %) also important. In summer and autumn, the diet of *O. mossambicus* was also dominated by these three dietary items in varying quantities (dietary data for remaining seasons not shown). The diet of sympatric native species was predominantly carnivorous, except for *M. cephalus* which consumed vegetal matter and unidentified organic matter (Table 2). The bulk of the diet of *G. holbrooki* was terrestrial insects; a dietary item unutilised by other species except *A. butcheri*. Some dietary variation was displayed by each species between seasons, and importantly, ANOSIM demonstrated a highly significant ($p<0.001$) difference between the diet of *O. mossambicus* and all sympatric species in each season (spring global R = 0.44, summer global R = 0.695, autumn global R = 0.736), except for *M. cephalus* in spring ($p<0.01$). Classification of the mean volumetric contributions of the different dietary taxa revealed three distinct groups (Fig. 3). The first group consisted of the three seasonal *G. holbrooki* samples, in which diets consisted principally of terrestrial insects. The second grouping included the three *O. mossambicus* samples and the one spring *M. cephalus* sample. This group primarily ingested vegetal matter, algae, silt/biofilm and sand. The third group included all other samples from species that were primarily carnivorous. The diets of this group (including *H. compressa*, *A. butcheri*, *P. olorum* and *A. caudavittata*) included insect larvae (dipteran larvae and ephemeropteran nymphs) and Crustacea.

The mean temperature in the Chapman River increased from 23.1 °C (± 0.00 SE) in spring to 27.5 °C (± 0.11 SE) in summer, and decreased in autumn to 22.9 °C (± 0.06 SE), and decreased again in winter to

Table 1

Total number, percentage contribution, density and length range of *Oreochromis mossambicus* and six co-occurring species collected from the Chapman River in (a) spring, (b) summer, (c) autumn and (d) winter 2002/2003. NB: Dietary analysis was restricted to samples equal to or larger than five specimens.

	O. mossambicus	*G. holbrooki*	*A. butcheri*	*A. caudavittata*	*M. cephalus*	*H. compressa*	*P. olorum*
(a)							
Total specimens collected	76	220	16	7	5	134	140
Percentage contribution	12.7 %	36.8%	2.7 %	1.2 %	0.8%	22.4%	23.4%
Density (m^{-2} ± SE)	0.34 (± 0.022)	0.88 (± 0.169)	0.06 (± 0.013)	0.02 (± 0.006)	0.02 (± 0.006)	0.52 (± 0.125)	0.56 (± 0.121)
Length Range (SL)	32–44 mm	25–36 mm	31–134 mm	45–69 mm	28–56 mm	30–59 mm	24–44 mm
(b)							
Total specimens collected	1344	1333	1	18	1	65	14
Percentage contribution	48.4 %	48.0 %	~0 %	0.6 %	~0 %	2.3 %	0.5 %
Density (m^{-2} ± SE)	3.23 (± 0.292)	3.86 (± 1.828)	0.01 (± 0.003)	0.05 (± 0.007)	0.01 (± 0.002)	0.13 (± 0.058)	0.04 (± 0.020)
Length Range (SL)	30–40 mm	22–29 mm	137 mm	20–73 mm	101 mm	43–55 mm	15–25 mm
(c)							
Total specimens collected	847	428	–	1	–	44	1
Percentage contribution	64.1 %	32.4 %	–	0.1 %	–	3.3 %	0.1 %
Density (m^{-2} ± SE)	8.47 (± 3.530)	4.28 (± 0.680)	–	0.01 (± 0.010)	–	0.44 (± 0.080)	0.01 (± 0.010)
Length Range (SL)	9–63 mm	17–27mm	–	30 mm	–	28–57mm	28 mm
(d)							
Total specimens collected	84	23	16	–	9	25	88
Percentage contribution	34.3 %	9.4 %	6.5 %	–	3.7 %	10.2 %	35.9 %
Density (m^{-2} ± SE)	1.05	0.29	0.20	–	0.11	0.31	1.10
Length Range (SL)	18–112 mm	22–31 mm	19–139 mm	–	26–149 mm	28–69 mm	11–41 mm

Table 2

Number of dietary samples, mean stomach fullness and percentage dietary contribution by volume (and percentage occurrence in parenthesis) of *Oreochromis mossambicus* and six co-occurring species collected from the Chapman River in spring (October 2002).

Dietary sample Mean stomach fullness (± SE) *Prey type*	***O. mossambicus*** *n* = 12 5.4 (± 0.61)	***G. holbrooki*** *n* = 12 4.6 (± 0.58)	***A. butcheri*** *n* = 12 5.5 (± 0.45)	***A. caudavittata*** *n* = 7 5 (± 0.76)	***M. cephalus*** *n* = 5 5.4 (± 0.40)	***H. compressa*** *n* = 12 4.8 (± 0.53)	***P. olorum*** *n* = 12 5.1 (± 0.6)
Algae (Unicell/Filament)	60.9 (100)	17.6 (50.0)	0.8 (25.0)	–	14 (100)	37.8 (91.7)	25.2 (75.0)
Bacillariophyceae	3.7 (100)	1.0 (25.0)	–	–	6.6 (100)	1.9 (83.3)	0.6 (41.7)
Vegetal matter	10.9 (91.7)	1.4 (25.0)	5.5 (75.0)	0.1 (14.3)	18.1 (100)	1.3 (33.3)	5.6 (75.0)
Seeds	–	–	0.2 (8.3)	–	–	–	–
Porifera gemmules/spicules	–	–	–	–	0.8 (80.0)	–	–
Protozoa	–	–	–	–	1.9 (80.0)	–	–
Arachnida	–	5.7 (25.0)	–	–	–	–	–
Terrestrial insects	–	54.3 (83.3)	2.5 (33.3)	–	–	–	–
Coleoptera (larvae)	–	–	1.4 (8.3)	–	–	–	5.7 (8.3)
Diptera (larvae)	–	9.2 (41.7)	36.5 (83.3)	69.6 (85.7)	–	22.7 (66.7)	54.4 (75.0)
Diptera (pupae)	–	1.1 (8.3)	5.6 (33.3)	3.1 (42.9)	–	4.1 (16.7)	0.7 (8.3)
Trichoptera (larvae)	–	–	7.3 (33.3)	–	–	–	–
Ephemeroptera (nymphs)	–	–	9.7 (41.7)	0.9 (14.3)	–	4.1 (8.3)	–
Anisoptera (larvae)	–	–	–	11.4 (14.3)	–	–	–
Zygoptera (larvae)	–	–	–	–	–	6.9 (8.3)	–
Amphipoda	–	–	–	1.4 (14.3)	–	12.8 (16.7)	–
Ostracoda	0.8 (16.7)	–	1.0 (33.3)	0.2 (14.3)	–	–	–
Gastropoda	–	8.6 (8.3)	14.7 (33.3)	–	–	0.9 (16.7)	–
Teleost	–	–	–	6.9 (14.3)	–	–	–
Organic matter (not identified)	5.8 (100)	–	6.8 (75.0)	2.4 (57.1)	16.5 (100)	2.5 (50.0)	3.9 (83.3)
Silt/biofilm	12.0 (83.3)	0.5 (8.3)	–	–	15.4 (100)	2.2 (33.3)	1.6 (66.7)
Sand	4.0 (100)	–	4.0 (83.3)	1.6 (28.6)	16.3 (100)	0.5 (8.3)	0.7 (25.0)
Unidentified	2.0 (41.7)	0.7 (16.7)	4.2 (66.7)	2.4 (57.1)	10.6 (100)	2.2 (50.0)	1.5 (33.3)

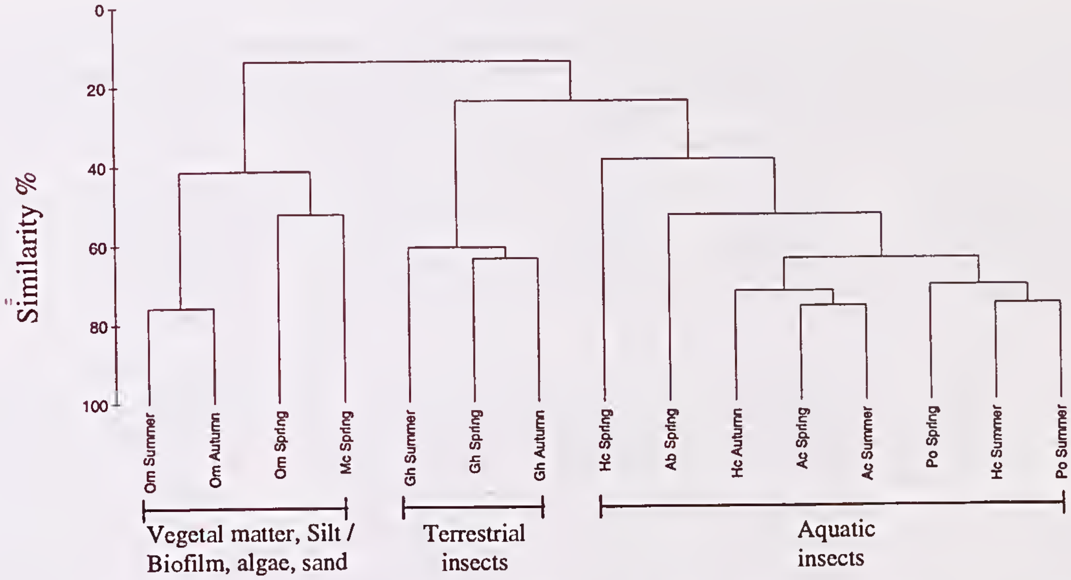

Figure 3. Classification of the mean volumetric contributions of the different dietary taxa of *O. mossambicus* and co-occurring species in the Chapman River in spring, summer and autumn 2002/2003. Species abbreviations are: Om = *O. mossambicus*, Ab = *A. butcheri*, Ac = *A. caudavittata*, Mc = *M. cephalus*, Hc = *H. compressa*, Gh = *G. holbrooki*, Po = *P. olorum*.

11.9 °C (± 0.01 SE) The mean pH in the Chapman River displayed little variation between spring (8.2 ± 0.00 SE), summer (8.5 ± 0.01 SE) autumn (8.6 ± 0.01 SE) and winter (8.6 ± 0.01 SE). Mean conductivity increased from spring (6.03 mScm^{-1} ± 0.023 SE) to summer (10.73 mScm^{-1} ± 0.031 SE), and again in autumn (11.90 mScm^{-1} ± 0.003 SE) before declining in winter (6.80 mScm^{-1} ± 0.005 SE).

Gascoyne River study site

Oreochromis mossambicus was collected from large tracts of the Gascoyne river system (Fig. 2). The dietary study site, Rocky Pool (114.138°E, 24.756°S), is a small riverine pool with a maximum depth of approximately 1.2 m situated 50 km east of the river mouth and the coastal town of Carnarvon. The benthic environment was dominated by the native macrophyte *Najas marina*. Netting was undertaken in standing pools downstream from Rocky Pool, approximately 3 km from the coast (113.671°E, 24.861°S), though *O. mossambicus* was not collected. *Oreochromis mossambicus* was found in permanent pools and artificial farm wells as far inland as Mt Augustus.

A total of 2404 fishes was collected from the Gascoyne River study site in one spring sample (22/10/2002). Four species were collected (Table 3), *i.e. O. mossambicus, M. cephalus, H. compressa* and *Leiopotherapon unicolor* (Terapontidae). *Oreochromis mossambicus* was the third most common species (though only marginally more abundant than *L. unicolor*) with a density of 0.03 m^{-2} (2.7 % of fish collected). Two distinct *O. mossambicus* size classes were present, *i.e.* specimens 165–198 mm, and 23–53 mm (Table 3). The most abundant species collected was, by far, *H. compressa* (1.2 m^{-2}, 89.4 % contribution). *Mugil cephalus* was the second most abundant species (0.08 m^{-2}, 6.2 % contribution). The terapontid *L. unicolor* comprised 1.7 % of fish collected, at a density of 0.02 m^{-2}.

Twenty prey items were identified from the intestinal tracts of *O. mossambicus* and three co-occurring species (Table 3). The primary food items consumed differed between *O. mossambicus* size classes. In contrast to small fish in the Chapman River, small fish from the Gascoyne River were insectivorous consuming ephemeropteran nymphs (43.6 %) and dipteran larvae (19.5 %) (Table 3). Large fish (165–198 mm) consumed primarily vegetal matter (54.2 %) and silt (12.4 %). Two of the native species were mostly insectivorous, with *L. unicolor* consuming primarily dipteran larvae (36.2 %) and terrestrial insects (27.5 %), while *H. compressa* consumed dipteran larvae (35.4 %) and ephemeropteran nymphs (14.9 %). *Mugil cephalus* consumed sand (58.9 %) and vegetal matter (17.2 %). ANOSIM between species' diets revealed a highly significant (Global R = 0.736; $p<0.001$) difference between the diets of all species including the two *O. mossambicus* size classes. In the Gascoyne River, the recorded mean temperature was 28.7 °C (± 0.01 SE), pH 8.5 (± 0.01 SE) and conductivity 3.37 mScm^{-1} (± 0.003 SE).

Lyons River study site

Oreochromis mossambicus was collected from two sites on the Lyons River (Fig. 2). The study site, Cattle Pool (116.817°E, 24.278°S), is a small riverine pool near Mt Augustus. One hundred and twenty six fish were collected from the Lyons River study site in one autumn sample (02/05/02). Four species were captured (Table 4), *i.e. O. mossambicus, L. unicolor, Craterocephalus cuneiceps* (Atherinidae) and *Hypseleotris aurea* (Eleotridae). *Oreochromis mossambicus* and *C. cuneiceps* both comprised *ca* 40 % of collected specimens and occurred at a density of 6.25 m^{-2}. *Hypseleotris aurea* occurred at a density of 3.12 m^{-2} and contributed 19.8 % of the total catch. *Leiopotherapon unicolor* was the least common species with only one specimen collected.

Small *O. mossambicus* (12–27 mm) collected in the Lyons River consumed predominantly algae (13.3 %),

Table 3

Total number, percentage contribution, density, length range, number of dietary samples, mean stomach fullness and percentage dietary contribution by volume (and percentage occurrence in parenthesis) of *Oreochromis mossambicus* and three co-occurring species collected from the Gascoyne River in spring (October 2002).

	O. mossambicus	*O. mossambicus*	*L. unicolor*	*M. cephalus*	*H. compressa*
Total specimens collected	43	21	40	150	2150
Percentage contribution	1.8 %	0.9 %	1.7 %	6.2 %	89.4 %
Density (m^{-2} ± SE)	0.02 (± 0.006)	0.01 (± 0.001)	0.02 (± 0.009)	0.08 (± 0.085)	1.18 (± 0.410)
Length Range (SL)	23–53 mm	165–198 mm	69–105 mm	94–110 mm	24–49 mm
Dietary sample	*n* = 14	*n* = 13	*n* = 11	*n* = 9	*n* = 11
Mean stomach fullness (± SE)	5.5 (± 0.75)	5.2 (± 0.63)	6.5 (± 0.62)	4.1 (± 0.77)	5.1 (± 0.41)
Prey type					
Algae (Unicell/Filament)	5.1 (92.9)	7.4 (100)	–	6.7 (100)	7.7 (90.9)
Vegetal matter	3.8 (71.4)	54.2 (100)	2.1 (42.9)	17.2 (100)	0.9 (54.5)
Bacillariophyceae	1.0 (28.6)	1.1 (92.3)	–	1.2 (33.3)	0.2 (9.1)
Seeds	–	1.9 (7.7)	4.6 (35.7)	–	–
Nematoda	–	–	0.1 (7.1)	0.5 (33.3)	–
Terrestrial insects	2.3 (28.6)	4.5 (61.5)	27.5 (57.1)	–	1.0 (27.3)
Coleoptera (larvae)	1.3 (7.1)	–	–	–	–
Diptera (larvae)	19.5 (57.1)	–	36.2 (64.3)	–	35.4 (90.9)
Diptera (pupae)	0.1 (0.0)	–	5.1 (21.4)	–	1.1 (9.1)
Trichoptera (larvae)	–	–	1.3 (21.4)	–	11.0 (54.5)
Ephemeroptera (nymphs)	43.6 (92.9)	–	–	–	14.9 (27.3)
Copepoda	–	–	–	–	–
Ostracoda	1.5 (21.4)	0.2 (15.4)	12.5 (64.3)	1.3 (66.7)	11.2 (72.7)
Gastropoda	–	–	0.3 (7.1)	–	2.5 (18.2)
Teleost/invertebrate eggs	–	–	–	–	–
Teleost	–	–	7.0 (7.1)	–	–
Organic matter (not identified)	2.7 (57.1)	5.2 (100)	–	–	7.3 (81.8)
Silt / biofilm	12.4 (100)	21.5 (100)	–	13.3 (100)	2.9 (45.5)
Sand	4.4 (92.9)	1.2 (84.6)	0.6 (14.3)	58.9 (100)	0.8 (18.2)
Unidentified	2.4 (50.0)	2.8 (61.5)	2.8 (57.1)	1.0 (55.6)	3.2 (54.5)

vegetal matter (17.1 %) and silt/biofilm (42.5 %) (Table 4). A concordant diet was recorded for both sympatric, native species. *Craterocephalus cuneiceps* consumed primarily algae (14.8 %), vegetal matter (19.7 %) and silt/biofilm (42.0 %). Similarly, *H. aurea* consumed algae (14.7 %), vegetal matter (17.8 %) and silt/biofilm (41.8 %). Thus, all species predominantly consumed the same dietary items, *i.e.* most likely the same detrital matter. ANOSIM confirmed that no statistical difference existed between the dietary composition of all species (Global R = 0.018, p>0.05). In the Lyons River, the recorded mean temperature was 31.3 °C, pH 8.5 and conductivity 2.477 $mScm^{-1}$.

Lyndon and Minilya rivers study sites

Oreochromis mossambicus was collected from one site in the Lyndon River and two sites in the Minilya River (Fig. 2). The Minilya River (114.778°E, 23.908°S, sampled 2km east of Middalya Homestead) and the Lyndon River (113.964°E, 23.539°S, Learmonth Minilya Road) are intermittent rivers that drain into Lake McCleod during flood events. In the Minilya River, 132 *O. mossambicus* were collected with a length range of 43–117 mm, and a mean density of $0.72m^{-2}$. The only native species recorded was *L. unicolor* (132 specimens with a mean density of 0.90 m^{-2}). Forty-five *O. mossambicus* were collected from the Lyndon River (77–120 mm), with a mean density of 0.34 m^{-2}. No other species were collected. The salinity in the small drying pools in the Lyndon River was *ca* 149 $mScm^{-1}$, *i.e.* between two and three times the salinity of seawater.

Discussion

Distribution

The distribution of *O. mossambicus* is increasing in Western Australia, a pattern that has been observed in nonindigenous populations on the east coast of Australia as well as in many other countries (Arthington & Blühdorn 1994; Canonico *et al.* 2005). After the initial discovery of *O. mossambicus* in the Gascoyne River in 1981, the species quickly spread throughout this river and a major tributary, the Lyons River (Blühdorn & Arthington 1990). It is likely that this population originated from ornamental stock, though the affiliation of this group with the more recently discovered populations in Western Australia is unknown. The occurrence of *O. mossambicus* in the Chapman River was recorded in the Western Australian Museum records in 1992, though the species was originally noted from a farm dam in the Chapman River region in 1978. It is possible that this may be the source of the Chapman River population, through flooding or human intervention. It is likely that the absence of a barrier in the Chapman River (*i.e.* weir/gauging station) would have allowed the species to spread further upstream, as observed in the Gascoyne and Lyons Rivers.

Human intervention was cited by Blühdorn *et al.* (1990) as most likely responsible for multiple, isolated *O. mossambicus* populations in Queensland. Accordingly, nonindigenous populations of ornamental fishes are often found adjacent to populated areas (Lintermans 2004). It is therefore no surprise that *O. mossambicus* has

Table 4

Total number, percentage contribution, density, length range, number of dietary samples, mean stomach fullness and percentage dietary contribution by volume (and percentage occurrence in parenthesis) of *Oreochromis mossambicus* and three co-occurring native species collected from the Lyons River in Autumn (May 2002).

	O. mossambicus	***H. aurea***	***C. cuneiceps***	***L. unicolor***
Total specimens collected	50	25	50	1
Percentage contribution	39.7 %	19.8 %	39.7 %	0.01 %
Density (m^{-2})	6.25	3.12	6.25	0.12
Length Range (SL)	12–27 mm	20–33 mm	14–33 mm	60 mm
Dietary sample	$n = 12$	$n = 12$	$n = 12$	–
Mean stomach fullness (± SE)	4.8 (± 0.32)	6.1 (± 0.29)	5.25 (± 0.28)	–
Prey type				
Algae (Unicell/Filament)	13.3 (100)	14.7 (100)	14.8 (100)	–
Bacillariophyceae	8.3 (100)	9.3 (100)	8.1 (100)	–
Vegetal matter	17.1 (100)	17.8 (100)	19.7 (100)	–
Terrestrial insects/parts	0.6 (58.3)	0.4 (41.7)	0.5 (50)	–
Copepoda (larvae)	0.1 (8.3)	–	0.1 (8.3)	–
Organic matter (not identified)	10.1 (100)	9.1 (100)	8.6 (100)	–
Silt/biofilm	42.5 (100)	41.8 (100)	42.0 (100)	–
Sand	1.2 (100)	0.8 (83.3)	1.3 (83.3)	–
Unidentified	7.0 (100)	6.2 (100)	4.9 (91.7)	–

been found in the Chapman and Gascoyne Rivers which are both located adjacent to the large regional centres of Geraldton and Carnarvon, respectively. Flooding may also result in rapid range expansions, particularly as northwestern Australia experiences highly seasonal precipitation that results in intermittent watercourses and frequent localised flooding (Unmack 2001). Fish from the Gascoyne River are likely to have seeded populations in the Minilya and Lyndon rivers nearby, either through flooding and/or deliberate release. Although the Minilya and Lyndon rivers are not directly connected, these rivers are in close proximity and both drain into the same intermittent flood pan, Lake McCleod. During a flood event, Lake McCleod may have allowed individuals to colonise rivers that are not connected during dry periods.

Temperature is one of the most important environmental factors affecting the distribution of *O. mossambicus*. At 27°17' S, the *O. mossambicus* population in North Pine Dam in Queensland may be close to the southern limit of the potential range of this species because of low winter water temperatures (Arthington 1986; Blühdorn & Arthington 1990). The most southerly *O. mossambicus* population in Western Australia is located at a similar latitude (*ca* 28°45′ S). However, *O. mossambicus* may be able to populate habitats at considerably higher latitudes due to the ability to tolerate lower temperatures at higher salinities (Arthington 1986; Skelton 2001). In the freshwater North Pine Dam in southeastern Queensland, Blühdorn & Arthington (1990) noted fish kills when the temperature dropped below 14 °C. Juvenile (*i.e. ca* 50 mm) *O. mossambicus* were collected from the Chapman River in autumn and kept in large outside tanks (in freshwater) at Murdoch University until the following winter. At the onset of winter in Perth, a large proportion of these fish perished at between approximately 14 °C and 15 °C. However, *O. mossambicus* was collected, in good condition (*i.e.* not emaciated, and with full intestines), from the estuarine Chapman River in winter at temperatures of between 11.5°C and 12°C. It is also interesting to note that the natural range of the species in eastern Africa extends southwards from Mozambique to the Pongola River in freshwater (*ca* 27°S), and in brackish water further south to Algoa Bay at a latitude of *ca* 35°S (Loiselle 1996). Thus, the spread of *O. mossambicus* southwards, as speculated by Arthington (1986), may occur through the colonisation of estuarine environments.

Dietary analysis

Detritus dominated the diet of large *O. mossambicus* in the Gascoyne River, and smaller fish in the Chapman River. The detritus included algae, vegetal matter, Bacillariophyceae and quantities of inorganic matter including silt. De Silva (1985) noted that *O. mossambicus* was omnivorous, though a detritivorous diet was adequate for reproduction and normal growth in Sri Lankan reservoirs. Juvenile *O. mossambicus* often display a more carnivorous diet than mature fish (Bruton & Bolt 1975). The differing diets of small fish from the Gascoyne (insectivorous) and Chapman (detritivorous) Rivers is indicative of trophic plasticity that allows *O. mossambicus* to utilise various food sources (Arthington *et al.* 1994). Furthermore, although detritus typically has a low nutritional value, it is not usually resource limited and therefore allows *O. mossambicus* to utilise a common food source that many co-occurring native species, often carnivorous or omnivorous, will not consume.

ANOSIM demonstrated that the diets of *O. mossambicus* and co-occurring species in the Chapman and Gascoyne rivers were significantly different. Most native species in the Chapman River are carnivorous or omnivorous, and typically feed on or near the substrate. These species include *Acanthopagrus butcheri* (Sarre *et al.* 2000), *A. caudavittata* (Wise *et al.* 1994; Potter *et al.* 1994), *P. olorum* (Gill & Potter 1993) and *H. compressa* (Merrick & Schmida 1984), and similarly, in the Gascoyne River, the carnivorous *L. unicolor* and omnivorous *H. compressa* (Merrick & Schmida 1984). Thus, while no statistically significant dietary overlap exists, these native species and *O. mossambicus* inhabit and feed in similar areas. Blühdorn *et al.* (1990) also noted that in an artificial reservoir in Queensland, food resources were partitioned between *O. mossambicus* and two other species of comparable size; *i.e. Tandanus tandanus* (Plotosidae) and *L. unicolor. Oreochromis mossambicus* will often exploit an unrealised dietary niche, and as invasive species, detritivores are least likely to impact upon the colonised ecosystem (Moyle & Light 1996). Dietary analysis alone does not indicate that *O. mossambicus* competes with and disadvantages co-occurring native carnivorous and omnivorous fishes in these rivers.

Although the diets of all species captured in the Chapman and Gascoyne rivers were significantly different, the diets of *O. mossambicus* and the native species *C. cuneiceps* and *H. aurea* were very similar – in fact the dietary composition (Table 4) implies that all species were consuming the same detritus. *Craterocephalus cuneiceps* is a detritivore (Allen *et al.* 2005), however no data are available on the natural dietary preferences of *H. aurea*, though it is reasonable to assume a diet similar to that of the closely related omnivorous *H. compressa* (Merrick & Schmida 1984). It is very likely that in the restricted habitat of a small intermittent pool, the three species will utilise the same feeding areas and food resources, and if these are in short supply, they may compete for one or other resource, of both.

Potential ecological impacts

Although *O. mossambicus* has been declared a noxious species in some countries and parts of Australia, there is a paucity of research on its impacts on native fish (Arthington *et al.* 1994; Canonico *et al.* 2005). There is evidence that recruitment has declined in some co-occurring native species in Australia, and in areas where *O. mossambicus* thrives, few native species may be found (Mackenzie *et al.* 2001). Against this background, some generalisations can be made regarding the impact of the species in a Western Australian context. While breeding, male *O. mossambicus* become territorial and aggressive to their own species and others. At Rocky Pool in the Gascoyne River, males were observed guarding nests (*ca* 60–80 cm diameter) in the littoral zone, that had been cleared of macrophytes. The different antagonistic behaviours described by Turner (1986) were all observed. Most aggressive behaviour was directed towards other breeding males and to a lesser extent other fish. This territorial behaviour may not have a serious impact in areas with low densities of the introduced cichlid, however in the small residual pools of the Gascoyne River large areas of the substrate may be occupied by nests, restricting the movements of native species.

The variable seasonal densities of *O. mossambicus* in the Chapman River may influence the prevalence and distribution of native species within this system. At peak densities in autumn, *O. mossambicus* occurred at *ca* 8.5 fish per m^{-2} and contributed 64.1 % of fish collected. Native species were almost non-existent except for *H. compressa*. This phenomenon may be due to the displacement of indigenes by *O. mossambicus*, though it may also be influenced by the native species' biology. The size classes of the two rarest species, *A. butcheri* and *M. cephalus*, indicate that only juveniles were collected. Juveniles of these species may have increased in size and migrated to different estuarine habitats in subsequent sampling seasons and thus were not represented in our samples. Similarly, during reduced winter temperatures, *O. mossambicus* may occupy different habitats thus explaining the reduced densities of this species. Also, colder temperatures may increase the mortality of juveniles from the previous reproductive period, as observed in *O. mossambicus* populations in South Africa (Cochrane 1986). It is unknown how large *O. mossambicus* grows in the Chapman River, as the largest specimen collected (112 mm) was considerably smaller than fish collected in the Gascoyne River, and the species maximum size of *ca* 350 mm (Arthington & Blühdorn 1994). Larger fish may occupy different sections of the estuary, or the species may grow no larger when exposed to low temperatures at this high latitude. Under unfavourable environmental conditions, *O. mossambicus* populations may become stunted, with small maximum sizes and precocious reproduction (Fryer & Iles 1972; Blühdorn & Arthington 1990; James & Bruton 1992). Longer-term research is needed to determine if these variations in diversity and prevalence of introduced and indigenous fishes are a regular seasonal phenomenon, or whether native species are decreasing in diversity and abundance over longer periods.

The potential impacts of *O. mossambicus* are likely to be of greater severity in more northern rivers for two reasons. Firstly, milder winter temperatures may reduce the cold-induced mortality of juveniles from the previous reproductive season (Cochrane 1986). Indeed, it is possible that mild winter temperatures in northern populations may allow breeding year round. Secondly, the variable hydrological regime of intermittent rivers (such as the Gascoyne) in northern areas, concentrates fishes in small residual ponds where resource competition is more likely. The negative effects in these circumstances may be greater than in a perennial water body such as the Chapman River. Blühdorn *et al.* (1990) described the *O. mossambicus* population in the Gascoyne River as having a "low population density", though the species now appears abundant in the Gascoyne and Lyons rivers, and has become the dominant species.

The native species under greatest threat from *O. mossambicus* identified in this study are *C. cuneiceps* and *H. aurea*. Not only are these species likely to be competing for food and space in small intermittent pools, but both natives are endemic to Western Australia and have limited distributions. *Craterocephalus cuneiceps* is also found in the Gascoyne River but rarely co-occurs with *O. mossambicus* (Morgan *et al.* 2004, Allen *et al.* 2005). This may explain why *C. cuneiceps* is the most abundant and widespread species in the nearby Murchison River (which is free of introduced fishes), and why it occurs in such low densities in the majority of sites sampled in the Gascoyne River (Allen *et al.* 2005). The gudgeon *H. aurea* is found only in the Gascoyne/Lyons and Murchison Rivers, and is listed as 'conservation dependent' by the Australian Society for Fish Biology.

This study represents the first research on the dietary composition and possible ecological impacts of *O. mossambicus* in Western Australia. The results infer that, to varying degrees, *O. mossambicus* may negatively impact on native species through resource competition and agonistic behaviour. Furthermore, there is evidence of dietary overlap between *O. mossambicus* and endemic Western Australian species *C. cuneiceps* and *H. aurea*, both of which have restricted distributions. Considering the expanding range of *O. mossambicus* in Western Australia, it is likely that this trend will continue and a greater number of native fish communities and species will be exposed to this invasive cichlid.

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Where are they now? A baseline distributional description of introduced redclaw crayfish *Cherax quadricarinatus* (von Martens) in the east Kimberley region

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Abstract

A trapping survey in the wider Ord River catchment and adjacent river systems of the east Kimberley region between August and December 2006, failed to extend the distributional range of redclaw crayfish beyond Lake Kununurra, where it was first introduced in 1998. These findings suggest an opportunity remains for its control.

Keywords: redclaw crayfish; *Cherax quadricarinatus*; introduced species; translocation, Kimberley

Introduction

In 2000, redclaw crayfish *Cherax quadricarinatus* (von Martens) were first found in Lake Kununurra on the Ord River, and their introduction is the first recording of any freshwater crayfish species in Western Australia's Kimberley region (Doupé *et al.* 2004). Redclaw crayfish are a tropical species with a pre-European distribution thought to be confined to far northern Queensland and the northern and eastern parts of the Northern Territory (Riek 1969). In the Northern Territory, however, they have been translocated as far south-west as the Flora-Katherine-Daly River system (G Dally, Museum and Art Gallery of the Northern Territory, *pers comm*), but are thought to be absent from the Victoria River and those other river systems extending westwards to the Western Australian border (I Ruscoe, Northern Territory Department of Fisheries, *pers comm*).

Who translocated redclaw crayfish to the east Kimberley remains unknown and apart from the significant concerns for their probable ecological impact (*e.g.* Sala *et al.* 2000), this introduction has raised several questions including, what is the likelihood of them spreading into the wider Ord River system and beyond? And, where is the nearest population(s) of redclaw crayfish in the Northern Territory? In this paper I summarize the results of an extensive sampling program designed to provide baseline distributional data for redclaw crayfish in the east Kimberley region of northern Australia.

Materials and Methods

Between August and December 2006 I sampled the wider Ord River catchment and adjacent river systems for redclaw crayfish (Fig 1). My sampling program focussed on those waterways and fishing areas that are most readily accessible, and particularly by recreational anglers, because Australian Quarantine Inspection Service personnel occasionally confiscate redclaw crayfish from fishermen attempting to bring these animals from the adjacent Northern Territory for use as bait (Doupé *et al.* 2004). At each site (see Table 1 for details) I set 20 – 50 box-style (or opera house) crayfish traps baited with poultry pellets in replicate sets among recognizably different microhabitats for three consecutive nights. All traps were inspected every morning and re-set, regardless of trapping success.

Results and Discussion

I have been monitoring the upstream spread of redclaw crayfish in Lake Kununurra since 2002 and in August 2006 I found crayfish within 3 km of the Ord River dam wall (*i.e.* Lake Argyle), indicating they are now distributed throughout Lake Kununurra. Nevertheless, I did not capture any redclaw crayfish in any other river system or water body (including Lake Argyle) in the wider Ord River catchment outside Lake Kununurra, or elsewhere in the east Kimberley region.

During my years of trapping I have received anecdotal evidence for redclaw crayfish existing in the (lower) Ord River below Lake Kununurra, with anglers reporting remnant claws in the guts of barramundi (*Lates calcarifer* (Bloch)). Those claws that I have inspected, however, have been of cherabin (or freshwater prawn, *Macrobrachium* sp. L.) and the similarities in claw morphology between the two might mislead the untrained eye. Notwithstanding, cherabin are found throughout the downstream reaches of the lower Ord River and if redclaw crayfish are escaping there, it may be that predation of them by Ariid catfishes is limiting their dispersal (see Doupé *et al.* 2004; Morgan *et al.* 2004).

The nearest population of redclaw crayfish that I am

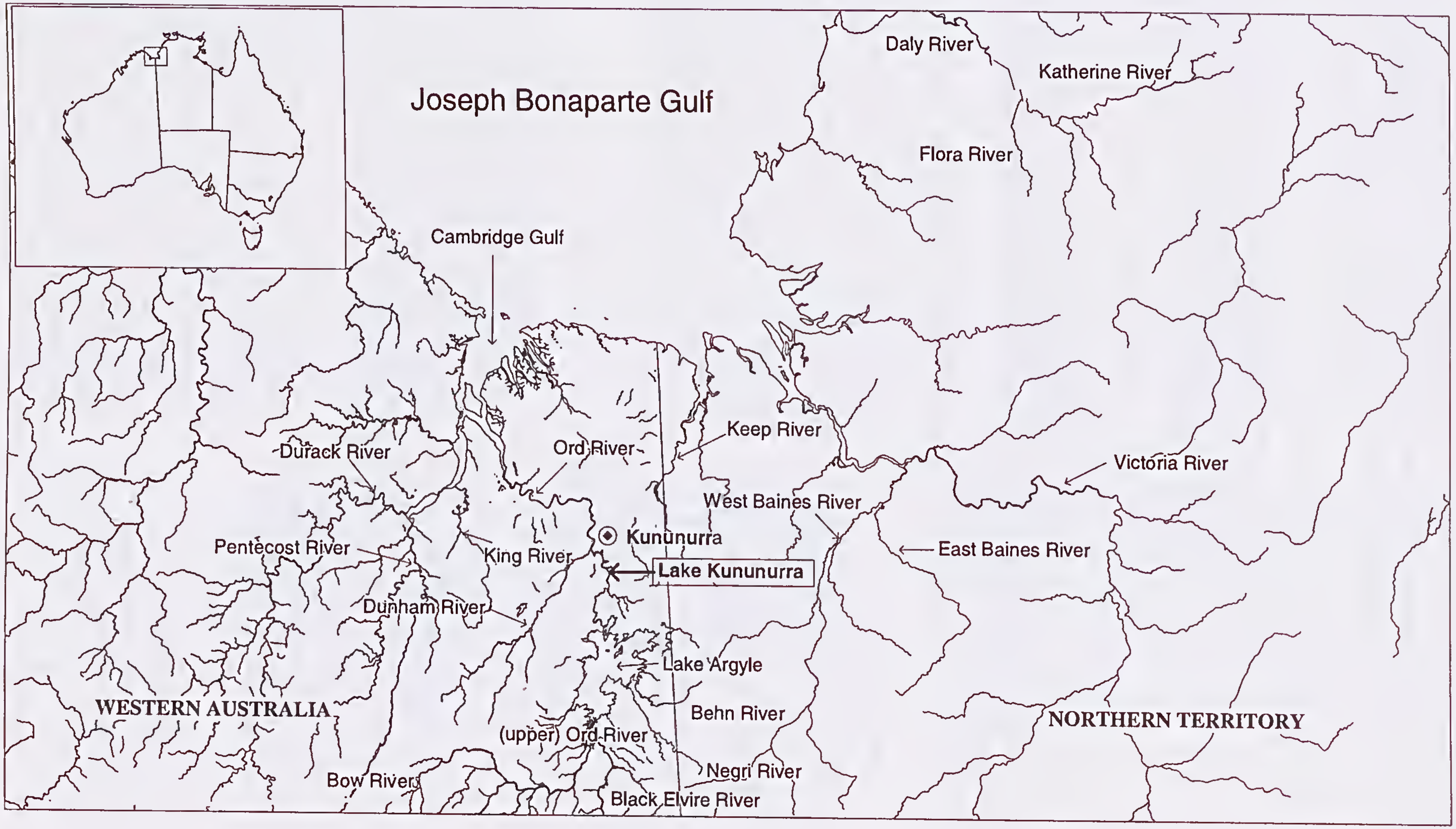

Figure 1. Geographic overview of river systems sampled for redclaw crayfish in the east Kimberley region of Western Australia and the Northern Territory. Note that redclaw crayfish were only found in Lake Kununurra and a detailed map of this lake can be found in Gill *et al.* (2006).

Table 1

Summary reference point locality details for the distribution of redclaw crayfish in watersheds of the east Kimberley region. (Further sample site information is available from the author).

River system	General Location	Latitude (S)	Longitude (E)
Ord River above Lake Argyle			
Behn River	Argyle Downs station billabong	16°45'	128°94'
Behn River	Duncan Road crossing	16°46'	128°05'
Negri River	Duncan Road crossing (downstream)	16°61'	128°04'
Ord River	No. 8 yards Spring Creek station	17°06'	128°06'
Ord River	Old station billabong	17°31'	128°83'
Black Elvire River	Palm Springs water hole	17°59'	128°64'
Ord River	Crossing to Bedford Downs station	17°40'	128°52'
Bow River	Lissadell station	16°68'	128°60'
Dunham River	Gorge on Doon Doon station	16°27'	128°16'
Dunham River	New bridge crossing	16°01'	128°48'
Dunham River	Excelsior Reach	15°82'	128°55'
Dunham River	Flying Fox Hole	15°80'	128°65'
Lake Argyle	Lake above Spillway Creek	16°06'	128°77'
Lake Argyle	Boat ramp area	16°10'	128°74'
Lake Kununurra	All tributaries and main channel	15°57'	128°46'
Ord River below Lake Kununurra			
Dunham River	Ord River junction	15°77'	128°68'
Ord River	Ford's Beach	15°75'	128°70'
Ord River	Ivanhoe Crossing	15°71'	128°67'
Ord River	Button's Crossing	15°68'	128°68'
Ord River	Skull Rock	15°67'	128°70'
Ord River	Carlton Crossing (upstream)	15°56'	128°58'
Other Cambridge Gulf Rivers			
King River	No.1 billabong	15°55'	128°11'
King River	Moochalabra Dam	15°56'	128°10'
Pentecost River	Upstream of crossing	15°73'	127°86'
Durack River	Jack's Hole billabongs	15°54'	127°66'
Joseph Bonaparte Gulf Rivers			
Keep River	Upstream of Legune station crossing	15°45'	129°03'
Keep River	Downstream of Legune station crossing	15°45'	129°03'
West Baines River	Fish Hole, Amanbidgi (Kildurk station)	15°75'	129°85'
East Baines River	Victoria Highway crossing	15°52'	130°08'
East Baines River	Auvergne station billabongs	15°59'	130°05'
Victoria River	Timber Creek (caravan park area)	15°40'	129°20'
Victoria River	Coolibah station billabong	15°41'	130°22'
Victoria River	Jasper Gorge	15°45'	130°25'
Victoria River	Dashwood Crossing	15°76'	131°05'
Victoria River	Pigeon Hole out station	15°84'	131°06'
Victoria River	Camfield River/station crossing	15°97'	131°09'
Victoria River	Wave Hill crossing (Kalkarindji)	16°45'	131°05'
Victoria River	Roadhouse/Victoria Highway crossing	15°41'	130°10'

aware can be found approximately 300 km to the north-east of Kununurra in the Flora River, a tributary of the Daly River (Fig 1). My failure to trap any redclaw crayfish in any of the river systems extending north and eastwards of Lake Kununurra, including the Victoria River, suggests that there is a substantial buffer between this introduced population and the nearest conspecifics.

The results of this survey also suggest that redclaw crayfish continue to exploit niche space within Lake Kununurra, although I suspect that this is not without impact. For example, since 2002 I have observed a steady decline in the once ubiquitous cherabin in the lake and now I very rarely trap them, suggesting that a significant reorganisation of the ecological community may be occurring there (see for example, Lodge *et al.* 1994; Shea & Chesson 2002). This evidence, although not quantified, may warrant further study of the ecological impacts of redclaw crayfish in Lake Kununurra.

The apparent isolation and confinement of redclaw crayfish to Lake Kununurra indicates that the management opportunity remains to contain them to this water body and perhaps attempt to rid this species from the Kimberley.

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Winter bird assemblages across an aridity gradient in south-west Western Australia

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Abstract

Avian assemblages of eight sites located along a 625km gradient across south-west Western Australia were recorded during the winters of 2004 and 2006. The total number of species observed was 92, with 10 sighted only in 2004, 14 sighted only in 2006, with the remaining 68 sighted during both survey periods. Measures of site species richness, diversity and evenness were determined for each site and for each sampling year and the turnover rates of avifauna species categorized as either sedentary or locally nomadic versus either migratory or nomadic between years were determined. The similarity between avifauna assemblages was determined by Detrended Correspondence Analysis and related to environmental data by correlation analysis and analysis of variance. Assemblage similarity between years at each site was greater than similarity between adjacent sites in the same year. However, avifauna similarity was related more to average annual precipitation than geographic proximity and was secondarily influenced by the presence of flowering trees and shrubs. There was no relationship between position on the geographic gradient and bird assemblage richness, diversity, evenness or dominance. Turnover rates between years of sampling of the regionally-nomadic and migratory species were significantly higher than sedentary and locally-nomadic species. A number of species showed discontinuous distributions in the central Wheatbelt, further documenting the impact of clearing on the avifauna of southwestern Western Australia.

Keywords: Avifauna richness, diversity, evenness and dominance, detrended correspondence analysis, inter-annual variation, species turnover rates, aridity gradient, south-west Western Australia

Introduction

The south-west corner of Western Australia has long been recognised as forming a natural floristic (Beard 1990) and faunal (Kikkawa & Pearse 1969) region. The extended geologic history and isolation from other similar climatic regions has allowed a long period for the Western Australian fauna to evolve close interactions with the vegetation and other organisms. However, Beard's (1990) South-West Botanical Province is not a strictly uniform region of vegetation and gradually changes, structurally and floristically, to the east and north. The vegetation changes have been related to the gradually declining rainfall (Beard 1990). Although Kikkawa & Pearse's (1969) South-western Faunal Sub-region overlaps this botanical province, it is not well known whether the avifauna assemblages also show such gradient changes. Eastern and northern Australian studies on bird assemblages have generally shown poor cohesion between the vegetational communities and avifaunal assemblages (Woinarski *et al.* 1988; Recher *et al.* 1991). However, Abbott (1999), using original distributions by Storr (1991), shows some evidence that the Western Australian central Wheatbelt once had higher species richness than regions of the Jarrah and Wandoo forests to the west and more arid regions to the east.

The objectives of this study were: 1) to document the winter assemblages of the avifauna in a range of sites along a gradient of increasing aridity; 2) to consider variation between two different years of sampling; 3) to relate patterns of avifauna distribution to particular environmental conditions.

Methods

Study sites

Observations were made at eight avifauna-sampling sites (Fig. 1). The end points of the sampling gradient were approximately 625km apart (825km by road) and covered an annual mean precipitation range from 1050mm at Mundaring to 230mm at Leinster (Table 1). Although the sites were on average 118 ± 64 km apart, there was a large decrease in rainfall from Mundaring to Durokoppin and then a more gradual decrease in total annual precipitation over the five remaining sampling sites. Local rainfall in the three months (April–June) preceding the 2004 sampling was significantly higher than the corresponding period preceding the 2006 sampling (paired $t = 2.80$, $p \leq 0.05$).

Although the vegetation species composition varied

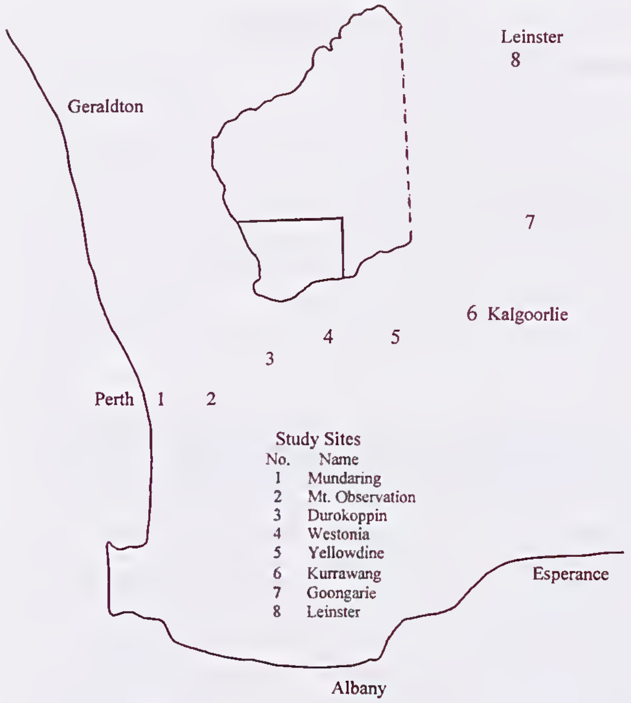

Figure 1. Approximate geographic position of the eight avian sampling sites in south-west Western Australia.

between sites, all sites chosen had a single canopy stratum dominated by eucalypt species, an understorey of shrubs and a litter layer that indicated a several-year period without fire (Table 2). Care was made to sample an area typical of the regional vegetation. A subjective assessment of the relative availability of flower resources was made during each sampling.

Sampling

At each avifauna-sampling site, bird observations were recorded over six separate time periods consisting of three early morning and three late afternoon sessions, each of two hours duration. All field observations were undertaken by the first two authors working together to share observation and recording. The area sampled was estimated using pedometer walking distances and a lateral observation region of 25 m on each side of the walking line. Census data were obtained by walking slowly forward, stopping to identify birds observed by sight and then proceeding when all birds at that location were recorded. Using this technique, area of sampling was determined to be between 15 and 21 ha for the range of sampling sites (Table 1).

Preliminary analysis of the bird richness data indicated that the total of 12 hr of observation was sufficient to maximize completeness of the sample as 90% of the final site richness value was always achieved after ≤8 hr and 95% after ≤10 hr of observation. The precautions of Watson (2003) were also followed to ensure the sampling area was representative of the regional vegetation and sampling effort was comparable between study sites. All field sampling was carried out between 14 July and 12 August 2004 and 16 July and 22 August 2006, proceeding sequentially from Mundaring to Leinster in each sampling year. Windy and rainy days were avoided, so the time required to complete the three morning and three afternoon samples took between three and five days at each site.

Site avifauna richness was the total number of bird species recorded at each site during the three-day sampling period. Three measures of site species heterogeneity were calculated. The Shannon indices of diversity ($H' = -\Sigma p_i \log_{10} p_i$) and evenness ($J' = H'/H'_{max}$) and the Simpson index of dominance ($D = \Sigma p_i^2$), where "p_i" equals the proportion for the ith species, combine information on both species richness and species evenness (Peet 1974). The Shannon indices are biased towards species richness, while the Simpson index of dominance is biased toward the abundance of the most common species (Magurran 1988). Statistical comparisons between the sample species diversity values employed the method of Hutcheson (1970). Spearman's rank correlation tests were used to compare patterns of avifauna assemblage characteristics. Site richness, evenness and dominance between-year comparisons were made by correlation analysis.

The total number of observations recorded during the 12 hr of sampling was determined and the percentage recorded for each species provided the matrix of data for comparisons of avifauna assemblage structure between sites and years by Detrended Correspondence Analysis (DCA) using CANOCO version 3.11.5 (Jongman *et al.* 1995). Paired t-tests were used to determine differences

Table 1

Study site locations for avian observations. Mean annual rainfall (mm) and the rainfall of the three months preceding the sampling period approximated from data from nearest weather station (Australian Bureau of Meteorology – www.bom.gov.au/climate). Estimated area sampled (ha) determined from mean pedometer readings and 50m sampling width. Distance by road from Mundaring is also provided.

Site No.	Site Name	Longitude-Latitude	Annual Rainfall	Seasonal Rainfall 2004	Seasonal Rainfall 2006	Area (ha)	Distance (km)
1)	Mundaring	116° 11'E 31° 55'S	1050	330	108	15.0	0
2)	Mt. Observation	116° 31'E 31° 53'S	460	174	64	15.8	45
3)	Durokoppin	117° 31'E 31° 25'S	330	123	45	16.4	180
4)	Westonia	118° 41'E 31° 15'S	310	127	83	21.0	270
5)	Yellowdine	119° 39'E 31° 17'S	290	82	49	21.0	320
6)	Kurrawang	120° 25'E 30° 45'S	260	33	26	21.6	495
7)	Goongarrie	121° 10'E 29° 55'S	250	62	16	20.0	605
8)	Leinster	121° 45'E 27° 45'S	230	56	4	21.7	825

Table 2

Characteristics of bird observation sites including dominant tree species, common genera of the shrub layer, important features of the ground layer, and subjective assessment of relative amounts of flowering.

Site No.	Name	Tree Layer ≥3m	Shrub Layer >10cm<3m	Litter/Ground ≤10cm	Flowering	
					2004	2006
1)	Mundaring	*Eucalyptus marginata* *Corymbia calophylla*	*Dryandra sessilis* + many other spp.	Mostly covered by leaves, twigs	++++	+++
2)	Mt. Observation	*E. wandoo* *E. accedens*	*D. sessilis* + many other spp.	Occasional litter, mostly exposed gravel	+++	++
3)	Durokoppin	*E. salmonopholia* *E. loxophleba*	*Dryandra, Hakea* *Melaleuca,* *Allocasuarina*	Scattered litter in woodlands, sparse in shrubs	+	–
4)	Westonia	*E. transcontinentalis* *E. longicornis* *E. salubris*	*Melaleuca, Santalum* *Hakea,* *Allocasuarina*	Some dense areas of leaves, twig, others sparse	++	–
5)	Yellowdine	*E. salubris* *E. transcontinentalis*	Scattered *Melaleuca* *Hakea, Acacia*	Sparse litter layer	+	++
6)	Kurrawang	*E. lesouefii* *E. clelandii* *E. transcontinentalis*	*Acacia, Maireana* *Atriplex* *Melaleuca*	Litter under trees, very sparse elsewhere	+++	+
7)	Goongarie	*E. oleosa*	*Acacia, Allocasuarina* *Triodia*	Litter with mallees sparse elsewhere	+	–
8)	Leinster	*E. gongylocarpa* *E. kingsmillii* *E. oldfieldii*	*Dodonea, Cassia* *Grevillea* *Triodia*	Sparse litter, mostly under mallees	–	++

in axis position for sites between years. Correlation analysis was used to compare the DCA site axis scores with a range of the geographic, environmental and avifauna data.

For each site, avifauna species turnover rate was determined between sampling years as $T = 100[(d+a)/s]$, where "d" is the number of local departures (number of species not recorded at the site during the 2006 survey, but had been recorded during the initial 2004 survey), "a" is the number of local arrivals (number of species recorded at the site during 2006, but not recorded during the 2004 survey), and "s" is the total number of species observed at the site during both survey periods (Maron *et al.* 2005). Turnover rates between 1) the total, 2) sedentary and locally nomadic, and 3) migratory and nomadic species classes were compared by analysis of variance.

Results

Patterns of avian observations

A total of 92 species were recorded in the two surveys of the eight sites along the 625 km aridity gradient across south-west Western Australia (Appendix 1). Ten species were sighted only in 2004 and 14 species sighted only in 2006, with the remaining 68 species sighted during both survey periods. No species was recorded during both sampling years in all eight sites, however, the Weebill was sighted in 15 of the 16 samples and the Australian Ringneck and the Australian Raven were recorded in 14 of the 16 samples. Other widely occurring species recorded in at least 12 of the 16 samples were the Brown Honeyeater, Grey Shrike-thrush, Red Wattlebird, Striated Pardalote, Pied Butcherbird and the Yellow-throated Miner.

Although many were widespread, some species with low or high species DCA scores favoured the moister or drier ends of the aridity gradient. For example, the New Holland Honeyeater was the most commonly observed bird in the Jarrah forest study site at Mundaring, accounting for more than a quarter of the observations in both sampling years. Other species with predominant observation percentages in the Mundaring and Mt. Observation samples were the Red-capped Parrot, Western Spinebill, Scarlet Robin and Western Thornbill.

The most commonly observed birds of the central Wheatbelt and Goldfield woodlands sites were the widespread Red Wattlebird, Weebill, Australian Ringneck, Yellow-throated Miner and the Striated Pardalote, along with the more restricted regional species, the Chestnut-rumped Thornbill, White-eared Honeyeater and Yellow-rumped Thornbill. Species with high species DCA axis 1 scores were the commonly observed species recorded at the most arid end of the gradient. These included the Yellow-throated Miner, Crested Pigeon and Little Crow.

The first axis of the DCA site ordination, which explained 26% of the avifauna assemblage variation, separated the southwestern sites on the low score end of the axis and the northeastern sites on the high score end of the axis (Fig. 2). Sites of the central Wheatbelt tended

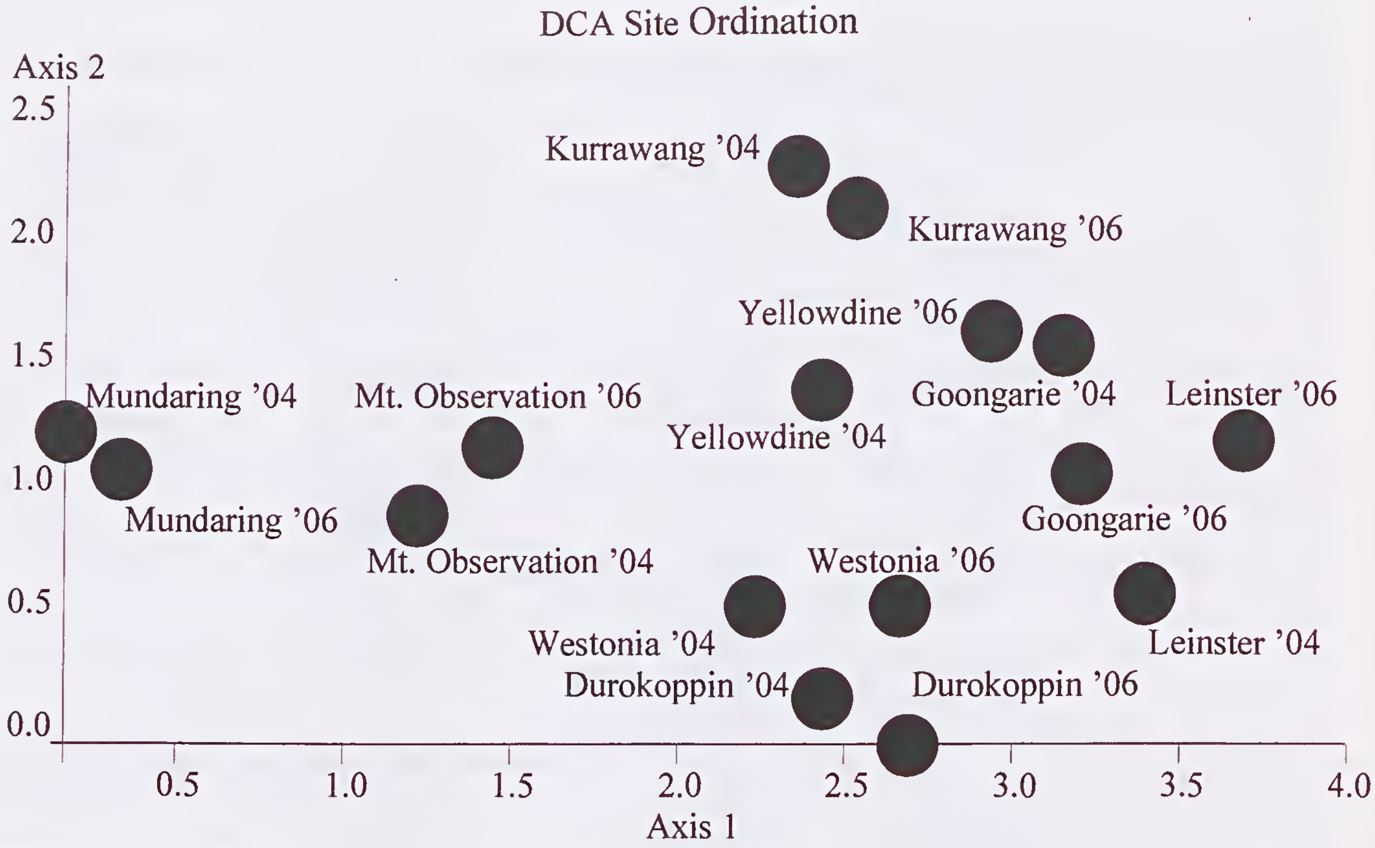

Figure 2. Sample positions on first and second Detrended Correspondence Analysis ordination axes.

to be in the central region of axis 1, but were separated with the Durokoppin samples at the lower score end of axis 2 and the remaining samples appeared sequentially as in their geographic position with increasing axis 2 scores. The second DCA axis explained a further 12% of the avifauna assemblage variation. The two DCA ordination axes also revealed that for each site the assemblage similarity between years was greater than between geographically adjacent sites. The difference between axis 1 scores for the same site between years was significantly less than the mean axis 1 scores between adjacent sites (paired t = 2.28, $p \leq 0.05$). This was also true for DCA axis 2 values (paired t = 3.57, $p \leq 0.01$).

Bird assemblage characteristics

Bird assemblage characteristics varied between years and sites (Table 3). Richness of the samples ranged from low values of 15 at the Leinster site in 2004 and 20 species at the Goongarie site in 2006 to highs of 31 species recorded at Durokoppin in 2004 and 35 species recorded in Mt. Observation in 2006. However, there was no relationship between site richness in 2004 and site richness in 2006 (correlation analysis $r = 0.35$, $p > 0.05$). The Shannon species diversity of avifauna samples ranged between 0.87 for the 2006 Goongarie sample and 1.30 for the 2006 Mt. Observation sample, but the diversities at each site in 2004 were not significantly correlated with those measured in 2006 at the same site (r

Table 3

Avian site richness, Shannon indices of diversity and evenness, and Simpson index of dominance values. Shannon diversity values with different superscript letters are statistically different at p≤0.05 by the method of Hutcheson (1970).

	Location Name	Species Richness		Shannon Indices Diversity		Evenness		Simpson Index Dominance	
		2004	2006	2004	2006	2004	2006	2004	2006
1)	Mundaring	23	32	1.11^{cd}	1.19^{ef}	0.83	0.79	0.12	0.11
2)	Mt. Observation	26	35	1.09^{cd}	1.30^{g}	0.77	0.84	0.12	0.07
3)	Durokoppin	31	32	1.24^{fg}	1.13^{de}	0.81	0.76	0.09	0.12
4)	Westonia	24	31	1.05^{c}	1.25^{fg}	0.76	0.84	0.13	0.08
5)	Yellowdine	29	34	1.19^{ef}	1.28^{g}	0.82	0.83	0.09	0.07
6)	Kurrawang	24	28	0.96^{b}	1.12^{d}	0.69	0.77	0.16	0.16
7)	Goongarrie	27	20	1.10^{cd}	0.87^{a}	0.77	0.66	0.12	0.27
8)	Leinster	15	25	0.96^{b}	1.09^{cd}	0.82	0.78	0.14	0.11

= 0.16, $p > 0.05$). Species diversities between years for individual sites showed statistically differences, however, overall diversity for 2004 was not different compared to 2006, as diversity increased at six sites in 2006, but decreased at two sites. As with the richness and diversity values, there were no overall differences between sampling years for evenness ($r = 0.11$, $p > 0.05$) and dominance ($r = 0.22$, $p > 0.05$). Also, sites, which ranked high in 2004, did not necessarily rank high in 2006 for richness (Spearman rank correlation $r = 0.21$, $p > 0.05$), diversity ($r = 0.28$, $p > 0.05$), evenness ($r = 0.04$, $p > 0.05$) or dominance ($r = 0.30$, $p > 0.05$). Although the DCA ordination indicated that the bird species composition changed between Mundaring and Leinster, the characteristics of richness, diversity, evenness and dominance between sites showed no gradient trends.

Species turnover between years averaged 45% for all birds, 40% for birds categorized as sedentary or locally nomadic and 60% for birds categorized as migratory or nomadic (Table 4). The degree of bird assemblage turnover of migratory and nomadic species was statistically greater than the turnover of sedentary and locally nomadic species (ANOVA $F_{d.f=21,2} = 3.65$, $p \leq 0.05$).

Table 4

Bird assemblage species turnover between years at the eight sampling sites. Percentage turnover values for 1) all birds (All), 2) birds categorized as sedentary or locally nomadic (Sed/LocNom) or 3) migratory or nomadic (Mig/Nom) are presented for the mean±se of all sites and for each site individually.

Site	Species Turnover Percentage All	Sed/LocNom	Mig/Nom
All Sites – mean±se	44.9±3.4	40.0±4.3	59.1±7.3
1) Mundaring	42.9	26.1	75.0
2) Mt. Observation	50.0	51.9	46.2
3) Durokoppin	29.7	22.2	50.0
4) Westonia	42.9	33.3	63.6
5) Yellodine	34.2	37.0	33.3
6) Kurrawang	54.3	54.2	54.5
7) Goongarie	48.4	47.8	50.0
8) Leinster	57.1	47.8	59.1

Gradient relationships

Variation in avifauna assemblage structure was most strongly related to annual rainfall (Table 5). Annual rainfall had a slightly higher correlation with the first DCA axis site scores than did the geographic separation from the western-most site to the other sites, measured as difference in the degrees of latitude and longitude. The correlation analyses also confirmed that there was no relationship between bird assemblage structure as defined by the DCA analysis with species richness, species diversity, evenness and dominance.

Avifauna assemblage structure was secondarily influenced by the presence of flowers as a food resource (Table 5). The second DCA axis of community variation showed this pattern with significant relationships with the percentage of observations of all the 14 honeyeater species to the total number of observation of all species and the number of members of the Meliphagidae observed in the site. The increase of locally nomadic honeyeater species into sites with high axis 2 scores led to a significant correlation between the number of honeyeaters and DCA axis 2 scores.

The generally drier conditions of 2006 compared to 2004 did not seem to influence bird assemblage variation, as there was no major division between sampling years on either of the two primary DCA axes. Rainfall in the three-month period just prior to sampling showed the same general pattern as the long-term annual rainfall totals for the sampling sites, although the correlation coefficient was less with the former variable.

Discussion

Gradient patterns

At continental scales, animal assemblages are generally more diverse in habitats that are more productive (Ricklets 1980). Tropical areas have more bird species than temperate areas and forests have more bird

Table 5

Correlations and level of probability with site DCA axis scores for selected geographic and environmental characteristics.

Characteristic	Axis 1	Prob.	Axis 2	Prob.
Annual rainfall (mm)	-.927	0.01	.001	n.s.
Site separation (degrees from Mundaring)	.833	0.01	.189	n.s.
3-month prior rainfall	-.745	0.01	-.185	n.s.
% Observations by spp. of the Honeyeaters	-.379	n.s.	.829	0.01
Turnover % of sedentary & loc. nomadic spp.	.299	n.s.	.582	0.05
Species diversity	-.287	n.s.	-.252	n.s.
Number of honeyeater species at site	-.283	n.s.	.742	0.01
Evenness	-.254	n.s.	-.230	n.s.
Species richness	.232	n.s.	.009	n.s.
Dominance	.209	n.s.	.157	n.s.
Turnover % of all species	.123	n.s.	.489	n.s.
Turnover % of nomadic and migratory spp.	.049	n.s.	-.181	n.s.
Total number of observations at site	.039	n.s	.114	n.s.

species than deserts. In the Northern Hemisphere, bird species diversity within more limited geographic areas is strongly related to the structural diversity (primarily the number of vegetation layers) of the habitat (MacArthur & MacArthur 1961; Moss 1978; James & Wamer 1982). In Australia, there is less agreement regarding habitat factors affecting avian species composition, richness and diversity (Ford 1989; Woinarski *et al.* 1997). In a limited study from eastern Australia, Recher (1969) found that foliage height diversity was an important determinant of bird species richness. However, in a study of several Western Australian wandoo woodland habitats, Arnold (1988) found that vegetation structural diversity was not such a strong determinant of avian diversity and suggested that floristic diversity was a more important factor affecting avian diversity at the regional scale. In the present survey, even though there was a gradual change in species composition from Mundaring to Leinster, there was no general trend in site richness and diversity characteristics despite the survey extending more than 625 km in length. Although there was a general decrease in canopy tree height and density over the aridity gradient, our findings support the broad conclusions of Keast (1985) that eucalypt communities throughout Australia vary little in total avian species diversity.

Inter-annual variation

Although the species composition of sites was more similar between years than between that of adjacent sites, the general lack of correspondence in site richness between years found in this study has been recorded previously. Species richness of Victorian woodland sites measured in 1994–95 and again in 2001–02 was unrelated, although bird densities were almost three times higher in the second sampling (Maron *et al.* 2005). Large annual population fluctuations, local absences and local influxes may be common events, especially in arid Australian habitats (James *et al.* 1995). Maron *et al.* (2005) reported a higher turnover of migratory and nomadic species than more sedentary species. There was a similar statistical difference in bird assemblage turnover values between these two categories in our study. Honeyeaters appear to be particularly erratic and habitats with flowers have generally been associated with large increases in honeyeaters (Ford & Paton 1985; Brown & Hopkins 1996; Franklin & Noske 1999), but not always (French *et al.* 2003). The number of honeyeater species at a site and the proportion of observations of honeyeaters to all bird species at the site were major determinants in the species assemblage variation along the second DCA site ordination axis in our study.

Conservation of avifauna in the central Wheatbelt

As a consequence of the destruction of significant areas of central Wheatbelt vegetation, the avifauna of this region has also lost significant components (Kitchener *et al.* 1982; Saunders 1989; Lynch & Saunders 1991) with vegetation remnants now dominated by a core of widely distributed, abundant and often highly competitive bird species. The records of a number of bird species of this study also showed distributions that were discontinuous in the central Wheatbelt region. These included the Yellow-plumed Honeyeater, Black-faced Cuckoo-shrike, Rufous Treecreeper, Golden Whistler and Grey Currawong. These species have been previously listed amongst other species that are now rare or extinct in the central Wheatbelt (Saunders & de Rebeira 1991; Birds Australia Western Australia n.d.). Long-term, detailed work at Durokoppin Reserve and other Wheatbelt remnants attribute the loss of these species and a number of others to the loss of native vegetation to agriculture (Saunders 1989; Saunders & Curry 1990). Durokoppin Reserve, however, was a survey site with relatively high richness and species diversity in our study. Saunders & de Rebeira (1991) suggest that remnant native vegetation blocks within mostly cleared agricultural land are actually carrying more species than they are capable of supporting over the long term and further species extinctions will inevitably occur from this region.

Our study indicates that the central Wheatbelt study sites are not currently richer in bird species compared to the more completely vegetated areas to the southwest and northeast, but our records do highlight gaps in the continuous distribution of a number of species. Protection of the present woodland remnants is essential to maintain the current level of bird species diversity in this region of south-west Western Australia.

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Appendix 1

Species composition, total number of observation and percentage of observations for each site for each year sorted by DCA species axis 1 scores. Common names and scientific nomenclature from Johnstone (2001), Johnstone & Storr (1998), (2004), Morcombe (2000) or Simpson & Day (2004). Status from Saunders & Ingham (1995), Morcombe (2000) and/or Simpson & Day (2004): S=Sedentary, L=Locally nomadic or migratory, N=Nomadic, M=Migratory. Detrended Correspondence Analysis Species Ordination axis 1 and 2 scores. Species with no scores were not included in the analysis (see text).

			Mundaring		Mt. Observation		Durokoppin		Westonia		Yellowdine		Kurrawang		Goongarrie		Leinster			
	Year of Observations	=	2004	2006	2004	2006	2004	2006	2004	2006	2004	2006	2004	2006	2004	2006	2004	2006	DCA	DCA
	Total Number of Observations	=	270	398	199	476	442	519	403	333	336	516	494	341	364	244	164	313	Axis 1	Axis 2
Common Name	Scientific Name	Status																		
New Holland Honeyeater	*Phylidonyris novaehollandiae*	L	28.3%	25.6%	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-56	112
Red-capped Parrot	*Platycerus spurius*	S	6.3%	10.3%	-.-	0.2%	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-51	105
Western Spinebill	*Acanthorhynchus superciliosus*	L	7.8%	10.6%	-.-	0.8%	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-49	107
Scarlet Robin	*Petroica multicolor*	L	7.4%	3.5%	1.0%	0.8%	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-44	118
Western White-naped Honeyeater	*Melithreptus chloropsis*	S	4.5%	2.3%	-.-	2.1%	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-29	116
Spotted Pardalote	*Pardalotus punctatus*	N	3.3%	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-
White-browed Scrub Wren	*Sericornis frontalis*	S	-.-	1.0%	0.5%	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-19	94
Golden Whistler	*Pachycephala pectoralis*	L	1.1%	0.2%	0.5%	-.-	-.-	-.-	-.-	0.3%	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-14	76
Short-billed Black Cockatoo	*Calyptorhynchus latirostris*	N	3.7%	-.-	4.0%	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-14	122
Western Wattlebird	*Anthochaera lunulata*	N	1.5%	3.0%	2.0%	1.3%	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-10	105
Western Thornbill	*Acanthiza inornata*	S	8.9%	3.5%	18.1%	5.7%	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	6	114
Silvereye	*Zosterops lateralis*	M/N	0.7%	0.8%	1.5%	1.1%	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	9	110
Laughing Kookaburra	*Dacelo novaeguineae*	S	0.4%	0.8%	0.5%	0.8%	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	0.3%	-.-	-.-	-.-	16	114
Splendid Fairy Wren	*Malurus splendens*	S	2.2%	0.5%	6.5%	0.8%	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	0.8%	1.3%	-.-	-.-	31	117
Wedge-tailed Eagle	*Aquila audax*	S	-.-	0.8%	-.-	0.2%	0.2%	-.-	-.-	-.-	-.-	-.-	0.2%	-.-	-.-	-.-	-.-	0.3%	42	124
Common Bronzewing	*Phaps chalcoptera*	L	0.4%	3.5%	-.-	2.3%	-.-	0.2%	0.2%	0.9%	1.8%	0.4%	0.2%	0.3%	-.-	-.-	-.-	-.-	46	133
Brown Honeyeater	*Lichmera indistincta*	L	7.8%	8.0%	12.1%	11.1%	3.6%	0.6%	-.-	-.-	4.4%	3.9%	4.3%	2.1%	-.-	-.-	1.2%	1.3%	50	170
Rainbow Lorikeet	*Trichoglossus haematodus*	N	1.5%	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-
Fan-tailed Cuckoo	*Cacomantis flabelliformis*	M/N	-.-	0.2%	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-
Tawny-crowned Honeyeater	*Phylidonyris melanops*	N	-.-	-.-	1.0%	1.3%	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	56	110
Mistletoe Bird	*Dicaeum hirundinaceum*	N	-.-	0.2%	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	0.3%	-.-	-.-	-.-	63	139
Western Corella	*Cacatua pastinator*	N	-.-	-.-	-.-	-.-	0.5%	-.-	1.7%	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	67	180
White-cheeked Honeyeater	*Phylidonyris nigra*	L	-.-	-.-	0.5%	10.3%	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	73	110
Grey Fantail	*Rhipidura fuliginosa*	M	-.-	0.8%	20.1%	4.0%	6.3%	4.2%	0.2%	0.3%	1.5%	0.2%	-.-	-.-	0.8%	-.-	-.-	-.-	74	0
Rufous Whistler	*Pachycephala rufiventris*	M	-.-	1.0%	1.5%	0.2%	-.-	0.4%	-.-	-.-	-.-	-.-	-.-	-.-	0.8%	1.3%	-.-	-.-	76	70
Painted Button-quail	*Turnix varia*	S	-.-	-.-	1.0%	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-
Rufous Tree-creeper	*Climacteris rufa*	S	-.-	-.-	1.0%	2.7%	-.-	-.-	-.-	-.-	0.9%	-.-	-.-	-.-	-.-	-.-	-.-	-.-	79	144
Australian Magpie	*Gymnorhina tibicen*	L	-.-	3.3%	1.5%	1.1%	0.7%	0.8%	-.-	0.6%	0.9%	-.-	0.4%	-.-	-.-	-.-	2.4%	1.6%	81	42
Grey Shrike-thrush	*Colluricincla harmonica*	S	2.2%	0.5%	0.5%	0.2%	0.9%	1.4%	2.7%	0.6%	-.-	1.0%	0.2%	1.2%	1.1%	-.-	-.-	-.-	94	22
Varied Sittella	*Daphoenositta chrysoptera*	S	1.5%	0.8%	2.0%	-.-	1.1%	1.2%	1.2%	1.8%	1.8%	0.8%	-.-	-.-	-.-	3.1%	-.-	-.-	107	10
Tree Martin	*Petrochelidon nigricans*	M	-.-	-.-	2.5%	8.2%	5.7%	4.0%	2.0%	3.9%	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	132	-63
Western Gerygone	*Gerygone fusca*	S	-.-	-.-	-.-	1.7%	-.-	1.2%	-.-	-.-	0.3%	0.6%	-.-	-.-	-.-	-.-	-.-	-.-	139	14
Red Wattlebird	*Anthochaera carunculata*	N	6.3%	4.5%	-.-	4.6%	1.1%	0.4%	9.9%	4.5%	12.0%	8.1%	28.1%	13.8%	5.4%	0.4%	-.-	-.-	150	262
Dusky Woodswallow	*Artamus cyanopterus*	M	-.-	-.-	-.-	3.2%	-.-	-.-	-.-	-.-	-.-	-.-	-.-	8.5%	-.-	-.-	-.-	-.-	195	333
Australian Ringneck	*Platycercus zonarius*	S	1.5%	4.0%	2.0%	4.2%	18.1%	16.4%	17.2%	15.6%	3.8%	3.3%	-.-	0.6%	0.8%	-.-	7.9%	1.3%	212	-80
Australian Raven	*Corvus coronoides*	S	0.7%	1.0%	1.5%	1.7%	0.9%	0.8%	4.7%	9.0%	8.5%	1.7%	1.6%	3.5%	-.-	-.-	1.2%	2.2%	220	108
Black-faced Cuckoo-shrike	*Coracina novaehollandiae*	L	-.-	0.8%	-.-	-.-	0.7%	0.4%	-.-	-.-	-.-	-.-	0.2%	1.8%	1.4%	-.-	0.6%	1.3%	220	205
Singing Honeyeater	*Lichenostomus virescens*	N	-.-	1.0%	0.5%	1.1%	0.2%	-.-	0.5%	-.-	-.-	-.-	3.8%	0.9%	4.8%	-.-	-.-	2.9%	229	243
Yellow-plumed Honeyeater	*Lichenostomus ornatus*	L	-.-	-.-	2.5%	8.0%	-.-	-.-	-.-	-.-	3.8%	11.1%	19.0%	26.4%	-.-	-.-	-.-	1.6%	250	329
Galah	*Cacatua roseicapilla*	S	1.5%	4.0%	-.-	0.2%	16.1%	19.1%	19.0%	10.2%	-.-	2.1%	-.-	-.-	-.-	-.-	14.6%	4.2%	257	-100
Willie Wagtail	*Rhipidura leucophrys*	L	-.-	-.-	-.-	0.4%	-.-	-.-	-.-	-.-	0.6%	0.2%	-.-	-.-	-.-	0.4%	-.-	0.3%	269	183
Grey Currawong	*Strepera versicolor*	S	0.4%	0.5%	-.-	-.-	-.-	-.-	2.7%	4.8%	1.2%	1.4%	-.-	-.-	1.4%	3.1%	-.-	-.-	272	5
Red-capped Robin	*Petroica goodenovii*	N	-.-	-.-	-.-	1.5%	0.2%	3.3%	0.5%	-.-	-.-	-.-	-.-	0.3%	-.-	2.2%	-.-	0.6%	276	-32

Yellow-rumped Thornbill	*Acanthiza chrysorrhoa*	S	-.-	-.-	-.-	1.9%	2.3%	3.7%	0.2%	0.6%	2.3%	2.3%	-.-	2.9%	-.-	-.-	-.-	1.6%	288	88
Weebill	*Smicrornis brevirostris*	S	-.-	1.3%	14.6%	13.0%	10.0%	19.6%	20.4%	14.1%	20.2%	10.3%	11.3%	11.4%	24.2%	48.7%	23.2%	11.8%	293	73
White-fronted Chat	*Epthianura albifrons*	N	-.-	-.-	-.-	0.8%	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-
Chimming Wedgebill	*Psophodes occidentalis*	S	-.-	-.-	-.-	-.-	0.2%	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-
Black-faced Woodswallow	*Artamus cinereus*	N	-.-	-.-	-.-	-.-	1.4%	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-
Western Yellow Robin	*Eopsaltria griseogularis*	L	-.-	-.-	-.-	-.-	0.5%	0.2%	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	296	-192
Jacky Winter	*Microeca fascinans*	L	-.-	-.-	-.-	-.-	0.9%	0.6%	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	300	-190
White-fronted Honeyeater	*Phylidonyris albifrons*	N	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	6.9%	-.-	-.-	-.-	-.-	0.3%	316	401
Elegant Parrot	*Neophema elegans*	L	-.-	-.-	-.-	-.-	2.0%	2.7%	-.-	2.4%	-.-	-.-	-.-	-.-	-.-	-.-	-.-	-.-	317	-147
Striated Pardalote	*Pardalotus striatus*	M	-.-	0.8%	-.-	1.9%	3.6%	1.5%	3.7%	2.7%	6.7%	5.2%	0.2%	3.2%	20.3%	1.3%	-.-	-.-	318	127
Purple-gaped Honeyeater	*Lichenostomus cratitius*	N	-.-	-.-	-.-	-.-	-.-	-.-	-.-	0.6%	-.-	0.2%	1.0%	-.-	-.-	-.-	-.-	-.-	325	281
Inland Thornbill	*Acanthiza apicalis*	L	-.-	0.8%	-.-	-.-	2.0%	0.4%	-.-	0.9%	0.9%	3.1%	-.-	2.6%	1.7%	6.6%	1.8%	1.6%	332	147
White-eared Honeyeater	*Lichenostomus leucotis*	L	-.—	-.—	-.—	-.—	6.3%	1.9%	5.4%	5.7%	2.6%	5.8%	4.0%	6.7%	4.8%	0.4%	-.—	-.—	333	142
Brown Falcon	*Falco berigora*	S	-.—	-.—	-.—	-.—	-.—	-.—	0.2%	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—
Horsfield's Bronze Cuckoo	*Chrysococcyx basalis*	M	-.—	-.—	-.—	-.—	-.—	0.4%	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—
Red-tailed Black-Cockatoo	*Calyptorhynchus banksii*	N	-.—	-.—	-.—	-.—	-.—	-.—	-.—	1.8%	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—
Peregrine Falcon	*Falco peregrinus*	N	-.—	-.—	-.—	-.—	-.—	-.—	-.—	0.6%	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—
Australian Owlet-nightjar	*Aegotheles cristatus*	S	-.—	-.—	-.—	-.—	-.—	-.—	-.—	0.3%	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—
Welcome Swallow	*Hirundo neoxena*	N/M	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	0.9%	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—
Major Mitchell's Cockatoo	*Cacatua leadbeateri*	S	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	4.7%	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—
Australian Pipit	*Anthus australis*	L	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	0.4%	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—
Black-shouldered Kite	*Elanus axillaris*	S	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	0.2%	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—
Square-tailed Kite	*Lophoictinia isura*	L	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	0.2%	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—
Pallid Cuckoo	*Cuculus pallidus*	M	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	0.2%	0.2%	-.—	-.—	-.—	-.—	-.—	337	326
Purple-crowned Lorikeet	*Glossopsitta porphyrocephala*	N	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	3.5%	4.8%	-.—	1.8%	-.—	-.—	-.—	-.—	337	261
Red Throat	*Pyrrholaemus brunneus*	S	-.—	-.—	-.—	-.—	-.—	-.—	-.—	0.9%	0.9%	-.—	-.—	-.—	-.—	0.4%	-.—	-.—	338	55
Blue-breasted Fairy Wren	*Malurus pulcherrimus*	S	-.—	-.—	-.—	-.—	-.—	-.—	-.—	2.4%	-.—	0.4%	-.—	0.6%	-.—	-.—	-.—	-.—	340	52
Regent Parrot	*Polytelis anthopeplus*	N	-.—	-.—	-.—	-.—	-.—	-.—	-.—	1.8%	0.6%	1.0%	-.—	-.—	-.—	-.—	-.—	-.—	341	45
Grey Butcherbird	*Cracticus torquatus*	L	-.—	-.—	0.5%	-.—	-.—	1.7%	0.5%	0.3%	1.5%	0.2%	-.—	0.3%	2.3%	1.8%	2.4%	-.—	345	31
Brown-headed Honeyeater	*Melithreptus brevirostris*	L	-.—	-.—	-.—	-.—	1.4%	0.8%	1.7%	3.6%	3.8%	4.5%	1.0%	2.3%	1.7%	4.0%	-.—	-.—	348	154
White-browed Babbler	*Pomatostomus superciliosus*	S	-.—	-.—	-.—	-.—	-.—	-.—	0.2%	1.8%	-.—	-.—	-.—	3.5%	5.4%	-.—	-.—	-.—	366	234
Chestnut-rumped Thornbill	*Acanthiza uropygialis*	L	-.—	-.—	-.—	-.—	4.8%	6.2%	2.7%	0.9%	12.9%	10.5%	0.2%	-.—	2.8%	5.3%	5.5%	7.3%	369	55
Spiny-cheeked Honeyeater	*Acanthagenys rufogularis*	N	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	0.6%	1.9%	1.4%	1.5%	7.6%	2.7%	-.—	0.3%	383	231
Hooded Robin	*Petroica cucullata*	S	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	0.2%	-.—	0.8%	-.—	-.—	-.—	385	232
Pied Butcherbird	*Cracticus nigrogularis*	S	-.—	-.—	-.—	-.—	2.0%	0.6%	1.2%	1.8%	0.3%	0.2%	0.6%	1.8%	0.3%	0.9%	9.1%	3.2%	401	25
Yellow-throated Miner	*Manorina flavigula*	L	-.—	-.—	-.—	-.—	5.2%	3.1%	1.0%	4.2%	-.—	-.—	13.6%	0.6%	8.2%	11.9%	18.3%	20.1%	407	144
Mulga Parrot	*Platycercus varius*	S	-.—	-.—	-.—	-.—	-.—	0.4%	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	1.2%	-.—	413	-55
Magpie Lark	*Grallina cyanoleuca*	S	-.—	-.—	-.—	-.—	0.2%	0.4%	-.—	-.—	0.6%	0.4%	0.4%	-.—	-.—	-.—	-.—	2.6%	421	172
Crested Pigeon	*Ocyphaps lophotes*	S	-.—	-.—	-.—	-.—	0.9%	1.7%	-.—	-.—	0.3%	8.9%	0.8%	0.3%	-.—	-.—	-.—	14.4%	429	182
White-winged Triller	*Lalage tricolor*	M	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	0.3%	-.—	-.—	-.—	-.—	-.—	-.—
Little Eagle	*Hieraaetus morphnoides*	S	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	0.3%	-.—	-.—	-.—	-.—	-.—	-.—
Brown Goshawk	*Accipiter fasciatus*	L	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	0.6%	-.—	-.—	-.—	-.—	-.—	-.—
Slender-billed Thornbill	*Acanthiza iredalei*	L	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	0.6%	-.—	-.—	-.—	-.—	-.—
Chestnut-breasted Quail-thrush	*Cinclosoma castaneothorax*	L	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	0.3%	-.—	-.—	-.—	-.—	-.—
Nankeen Kestrel	*Falco cenchroides*	S	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	0.6%	-.—	-.—	-.—
Crested Bellbird	*Oreoica gutturalis*	S	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	0.6%	1.3%	-.—	1.6%	453	141
Little Crow	*Corvus bennetti*	S	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	0.6%	2.7%	9.8%	16.6%	472	80
Western Bowerbird	*Chlamydera guttata*	S	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	0.3%	-.—	-.—
Red-backed Kingfisher	*Todiramphus pyrrhopygia*	N	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	-.—	0.6%	-.—	-.—

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